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FIG. 1.—*Lyginodendron Oldhamium.* Restoration. For description see text.

STUDIES

IN

FOSSIL BOTANY

BY

DUKINFIELD HENRY SCOTT

M.A., LL.D., PH.D., F.R.S., F.L.S., F.G.S., F.R.M.S.

LATELY HONORARY KEEPER OF THE JODRELL LABORATORY, ROYAL BOTANIC GARDENS, KEW

AUTHOR OF 'AN INTRODUCTION TO STRUCTURAL BOTANY'

"Nous devons donc envisager l'état présent de l'univers, comme l'effet de son état antérieur."—*Laplace.*

SECOND EDITION

VOL. I

PTERIDOPHYTA

CONTAINING 128 ILLUSTRATIONS

LONDON

ADAM AND CHARLES BLACK

1908

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PREFACE TO VOLUME I

THE exceptionally rapid progress of Fossil Botany during the last eight years has rendered necessary a very thorough revision of this book, and the rewriting of considerable portions. At the same time care has been taken to maintain the original character of the "Studies" as a first introduction to "those results of palæontological inquiry which appear to be of fundamental importance from the botanist's point of view." No attempt has been made to extend the scope of the book, which now, as before, is concerned essentially with the morphological and evolutionary aspects of Palæobotany, but in every chapter new results of research have been incorporated.

The volume now issued (Chapters I.-IX.) covers the Pteridophyta, *i.e.* those groups of Vascular Plants which may still be considered as, on the whole, Cryptogamic. The second volume (Chapters X.-XIV.) will contain the Spermophyta, so far as they are dealt with, together with the chapter on "General Results."

The boundary between Pteridophyta and Spermophyta, though no longer a "scientific frontier," happens to serve as a convenient limit between the two volumes.

The heading "Chapter" now replaces "Lecture," for, except perhaps in the Introduction, little trace of the original lecture form survives.

The first three chapters have been slightly re-arranged, so as to give a somewhat more logical division of the subject-matter. The substantial changes in these chapters are not great, Mr. Hickling's new observations on *Palaeostachya* and M. Halle's investigation of Mesozoic Equisetales being the chief novelties.

In Chapter IV. some account is given of a new type of fructification in *Sphenophyllum*, and Professor Nathorst's discovery of the group Pseudoborniales is shortly noticed.

In Chapter V. the changes are only in details, but Chapter VI. has received important additions; in particular, the curious seed-like fructifications of certain Palæozoic Lycopods, only shortly referred to in the first edition, have demanded fuller consideration.

In Chapter VII. a considerable advance in our knowledge both of *Sigillaria* and *Stigmaria* has been placed on record, and a short section on the herbaceous forms (Lycopoditeae) has been added, based on recent researches from French and Swedish sources.

The treatment of the Ferns (Chapters VIII. and IX.) has of necessity been profoundly changed by the discovery (due to Oliver, Kidston, Grand'Eury, White, and others) that so large a proportion of the supposed Palæozoic Ferns were, in reality, seed-bearing plants. Chapter IX., in which the now prominent family of the Botryopterideae is described, has been more extended than any other in the volume.

Volume I. contains 27 additional figures, besides a few cases in which new illustrations have been substituted for old. The figures now added are: 11, 27, 42, 47, 48, 76, 77, 78, 80, 81, 82, 83, 84, 94, 95, 103, 106, 114, 117, 120, 122, 123, 124, 125, 126, 127, and 128.

The new figures signed "R. S." are by my wife, Mrs. D. H. Scott, F.L.S., who has also made the Index.

D. H. SCOTT.

12*th March* 1908.

PREFACE TO FIRST EDITION

THESE *Studies in Fossil Botany* are founded on a special course of lectures, given, under the same title, at University College, London, in the year 1896.

The lecture form has been retained, but the number of lectures, into which the course is divided, has increased from eleven to fourteen. The introductory lecture preserves something of its original character, but all the rest have been completely recast, and most of them wholly rewritten.

At the present day, happily, fossil botany is an eminently progressive branch of science, and thus the mere lapse of time, since the lectures were delivered, has necessitated the introduction of much new matter and of many new points of view. A certain number of unpublished observations are also embodied in the book.

My object has by no means been to write a manual of fossil botany, a superfluous undertaking, in view of the excellent publications of the last few years. To mention only the very latest works, we have Mr. Seward's extensive treatise on *Fossil Plants*, now in course of publication, Professor Potonié's concise *Lehrbuch der Pflanzen-palæontologie*, and, within the present

year, M. Zeiller's *Éléments de Paléobotanique*, all of them, in their several ways, admirable hand-books for the student of palæobotany.

My purpose has been quite a different one, namely, to present to the botanical reader those results of palæontological inquiry which appear to be of fundamental importance from the botanist's point of view. Such far-reaching results have, at present, related almost entirely to two of the vegetable Subkingdoms, the Pteridophytes and the Gymnosperms, and it is to these Subkingdoms that the "Studies" are confined.

Within these limits, the value of the fossil evidence already available is manifest, though as yet hardly realised by botanists. The last few years, however, have seen a considerable advance in this respect, and we may hope that the palæontological record will no longer be ignored by students of the evolution of plants.

The present book, while it assumes no previous knowledge of fossil plants, presupposes a general acquaintance with recent botany, and with the rudiments, though only the rudiments, of geology. The terminology employed will be familiar to the botanical student; in the few cases where new or less usual terms are introduced, their explanation is given. Only two points seem to require notice here. The term *tracheae* is used in the wide sense adopted by De Bary, to cover both the *vessels* of the wood (arising by cell-fusion) and the *tracheides* (consisting of single cells).[1] Other authors have used the word in more

[1] De Bary, *Comparative Anatomy of the Phanerogams and Ferns*, English edition, 1884, p. 155.

restricted senses, but a general term for the water-conducting elements is indispensable, and De Bary's usage answers every purpose.

As in my *Introduction to Structural Botany*, the form *megaspore* is used throughout, in preference to *macrospore*, on the ground that the former term is more correct, and less liable to verbal confusion with microspore.

More than a third of the illustrations are new, and of these the majority (over forty in number) were drawn for me by Mr. Gwilliam, as indicated by his initials, G. T. G. In addition, a considerable number of the borrowed figures were redrawn by the same artist, to whose skill the book is much indebted.

Of the figures which are not new, a great many are taken from memoirs by the late Dr. W. C. Williamson, F.R.S., by myself, or by both of us, jointly. The source of all figures borrowed from other authors is of course acknowledged. I have to thank the Royal Society for permission to reproduce a large number of figures from the *Philosophical Transactions*, and the Linnean Society for a similar permission in the case of that Society's publications.

Mr. W. Carruthers, F.R.S., has kindly allowed me to make use of some illustrations from his well-known memoir on fossil Cycadean stems.

The restoration of *Lyginodendron Oldhamium*, forming the frontispiece, is the work of Mr. J. Allen, who has carried out a difficult task with much ability.

For various photographic illustrations I am indebted to Dr. E. C. Bousfield, and to my colleague, Mr. L. A. Boodle.

Wherever possible, I have given the number of the

section or specimen illustrated, in the collection to which it belongs. The abbreviation "Will. Coll." indicates the Williamson Collection (now in the British Museum, Natural History Department), while "S. Coll." refers to my own collection. In other cases the name is given in full.

The progress of scientific fossil botany has been greatly advanced by the skilled and intelligent work, in collecting petrified specimens and preparing sections, of such men as Mr. J. Lomax, Mr. G. Wild, and their colleagues, now deceased, Mr. J. Butterworth, Mr. J. Spencer, and others.

The references to the literature make no pretence to being exhaustive; I hope, however, that the works of chief importance to the botanical reader have been cited, and that justice has in all cases been done to those who have laid the foundations of our knowledge.

D. H. SCOTT.

20th June 1900.

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STUDIES IN FOSSIL BOTANY

CHAPTER I

INTRODUCTION

It is a general rule, applying to knowledge of every kind, that we cannot hope to understand any group of phenomena without a study of its antecedents. In political inquiries, no student would attempt to make himself acquainted with the existing constitution of a country, without seeking to gain a knowledge of the historical events by which it has been built up. In like manner, we cannot obtain any adequate idea of the present state of an art, such as sculpture or painting, unless we are prepared to study the history and development of the art in past times. Again, to come nearer to our own subject, scientific geography is impossible without geology, that is to say, without a knowledge of the past changes, to which the surface of the earth owes its present configuration. *Vere scire est per causas scire*, and causation is only known to us by the succession of events.

The same principle holds good for the special case of biology, the science of which botany is a part.

Botany, on its morphological side, consists in the application of the comparative method to the study of plants, with a view to the determination of their relationships. In these days, most of us, when we speak of relationship among organisms, mean to imply a real affinity, that is to say, a blood-relationship, so that, on this view, the ultimate object of morphological inquiry is to build up the genealogical tree of the organic world. Many attempts at the construction of genealogical trees have been failures, but still this is the object, however remote, which we have ultimately before us when we devote ourselves to morphological studies.

Existing organisms are related to each other more or less as brothers or cousins are related. All the species living at the present day belong, as it were, to the present generation. By the study of living organisms alone, it must necessarily be a matter very much of conjecture to decide which of them, in any given group, stands nearest to the old family stock. As regards some of the main taxonomic divisions, it is true, there can be no doubt. We should all agree, for example, that the Green Algae are, on the whole, much more primitive than the Flowering Plants ; but when we come to more difficult questions, such, for example, as the relative antiquity of the various families of Vascular Cryptogams, we find the most different opinions prevailing, and the conclusion at which we may arrive is largely a matter of subjective interpretation.

The only direct evidence which is possible in questions of descent among plants is from the ancient plants themselves. Fortunately, the rocks afford us a considerable amount of such direct evidence. I need

not say that the estimation of this evidence is in itself beset with the greatest difficulties, difficulties which those best appreciate who have themselves worked at fossil remains. The construction of a pedigree of the Vegetable Kingdom is a pious desire, which will certainly not be realised in our time; all we can hope to do is to make some very small contributions to the work. Yet we may at least gather up some fragments from past chapters in the history of plants, and extend our view beyond the narrow limits of the present epoch, for the flora now living is after all nothing but one particular stage in the evolution of the Vegetable Kingdom.

There is a phrase in the introduction to Count Solms-Laubach's admirable *Fossil Botany*[1] which I think very appropriate to our purpose. The author says that our object in studying fossil plants is "the completion of the natural system." That is the point of view which we shall take up in this book. I shall endeavour to bring before the reader those discoveries in fossil botany which already contribute something towards the completion of the natural system. If this be our purpose, it is evident that only well-characterised fossils have any interest for us. A specimen which may be an Alga, or perhaps a worm-track, or possibly even a wave-mark, is no doubt a curiosity, but will not help us much towards the end in view. Such specimens we shall leave severely alone!

Fossil botany at one time incurred a certain degree of not wholly undeserved contempt, from the excessive prominence given to doubtful objects, from which

[1] *Introduction to Fossil Botany*, English edition, 1892.

no conclusions of botanical interest could possibly be drawn.

The purpose which we have in view necessitates a botanical arrangement of our subject-matter, but it is essential for us also to bear constantly in mind the geological horizon of the remains with which we are dealing. In botanical history dates are just as important as in human history. In the former, however, absolute dates are unattainable, and only relative ages come into question.

The imperfection of the geological record is a familiar subject, and I need not dwell upon it here. We naturally find that vegetable remains are by no means evenly distributed throughout the series of strata. From some formations they are almost absent, while in others they are relatively abundant. Thus, beginning at the top, the Miocene is rich in such remains, especially in Switzerland ; so also is the Oligocene, as shown in the Isle of Wight, and the Eocene, to which the very rich leaf-beds in the Isle of Mull probably belong. All these Tertiary plants bear, as we should expect, a general resemblance to families now living.

Passing to the Secondary system, the Cretaceous formation is of special interest, for the first well-characterised Angiosperms make their appearance in these rocks. The remains from the Lower Greensand, however, are of a different type, and often have their structure well preserved ; they include some of the most remarkable of fossil forms. The Wealden, which some geologists reckon with the Cretaceous, and some with the Jurassic formation, yields abundant remains, with which we have become better acquainted through the work of

Prof. Seward of Cambridge. Ferns, Cycadophyta, and Conifers are the most characteristic forms of this period. The Oolitic strata, specially the Purbeck beds at the top of the system, also abound in Cycad-like remains, though most of the Mesozoic plants with the habit of Cycads were very different from any members of the family as now existing. The Wealden and Upper Jurassic of the United States are extraordinarily rich in Cycadophyta, recently investigated, with brilliant results, by Dr. Wieland of Yale. Such remains as we have from the Trias, *e.g.* the New Red Sandstone, have a still more old-world character (including strange and gigantic Horsetails and Lycopods), and prepare us for the Palæozoic system.

When we descend to the Permian we find ourselves at once among the characteristic Palæozoic families—especially the Sigillarias and Calamites, together with extinct Spermophytic types. This brings us to the Carboniferous formation, the flora of which is the richest and most remarkable which the rocks have preserved for us. The Carboniferous formation includes many other strata besides those of the Coal-measures, which belong to its upper part. The Coal-measures themselves reach a thickness of 12,000 feet, and represent a prodigious period of time. Fortunately, however, we are not limited for our specimens to this part of the formation, extensive as it is, for there are productive beds down to the base of the Lower Carboniferous rocks; when we find well-preserved plants much older than the Coal-measures, we may think ourselves specially fortunate. The plant-remains of the next great formation, the Devonian, though scanty compared

with those of the Carboniferous, are of the greatest interest, for this is the earliest period from which land-plants have come down to us in any abundance. It is very remarkable that in these early days we find not only well-characterised Vascular Cryptogams of various groups, but also highly organised Seed-plants, though not belonging to any family now living. There are probably no biologists left now who oppose *in toto* the doctrine of evolution, but if there were, they might draw a telling though fallacious argument from the high organisation of the Devonian flora. As regards the Silurian, there is little to say. Most remains from it are very doubtful, though there are one or two remarkable and well-preserved specimens, which have been shown on good evidence to belong to the Algae, while there is some evidence that even at this early period Vascular plants had already appeared.

To us, in these studies, the older formations will be the most interesting, for it is from them that we may expect to fill up gaps among the main groups of the natural system, and it is only with main groups that the limits of the book will allow us to deal. Also, I think that the investigation of the earlier formations (the Palæozoic and the Lower Mesozoic) has really been more fertile in results, up to the present time, than that of the later deposits, though no doubt from them also we may expect brilliant revelations in the future. The centre of gravity of our work will lie in the Carboniferous formation. The wealth of material which has come down to us from this period is marvellous, as every one knows. It is true, however, that the Coal-flora, rich as it is, is a very special one, although it extended with

a certain degree of uniformity over a large part of the earth's surface. It is essentially a swamp-flora, and we know little or nothing of the vegetation of the uplands. If we obtained all our knowledge of the existing flora from plants growing in such localities as the Great Dismal Swamp near the coast of the Southern United States, or from the mangrove-vegetation of tropical shores, our ideas would evidently be one-sided. On the other hand, when it is argued that on the hills of the Coal-period there may have been flowers and trees and shrubs of the higher Angiospermous families, that, surely, is a wild imagination. The flora of swamps, however peculiar, is made up of plants belonging to the same main groups as those of other habitats, and in so far as main groups alone are in question, we may take the Coal-flora, such as it has come down to us, as fairly representative of its period.

Before beginning our detailed work, we must say something as to the modes of preservation of fossil plants, without some knowledge of which we can form no idea of the relative value of the evidence before us.

There are two different modes of preservation, which we must keep perfectly distinct in our minds. These have been termed *incrustation* and *petrifaction*. Incrusted remains include almost all the specimens of fossil plants familiar to the general public. In the case of incrustation, the parts of plants were merely incased in the mineral substance, and any of the larger cavities they may have contained filled with it. Their organic tissue became converted into structureless coal, if it did not previously decay altogether. Hence, incrusted specimens give us impressions or casts,

which may reproduce with the greatest beauty an external or internal surface, but which tell us nothing of organised structure. The beautiful Fern-like fronds, so frequent in the Coal-measures, are perhaps more familiar to the ordinary observer than any other specimens of fossil plants. In them we have essentially the print of the frond on the shale lying above and below it. The finer the mineral material was when deposited, the more perfect will be the impression. The substance of the frond is reduced to a layer of coal in which there is little or no structure to be traced, though occasionally very resistant parts, such as spores or cuticle, will have left recognisable remains.

Other comparatively familiar fossils are the stems of the *Lepidodendra* and *Sigillariae*. In many of these specimens the markings of the surface, as characterised by the bases and scars of the leaves, are preserved exactly as in nature (see Figs. 54 and 86, pp. 130 and 207). Where this is the case the whole substance of the plant has been replaced by mineral matter. In other instances we have a *mould* of the external surface, elevations being represented by depressions, and *vice versa*. The markings, in all these cases, will necessarily depend on the state of preservation of the specimen when incrustation took place. Thus in *Lepidodendron* we have quite different superficial markings according to the condition of the specimen, whether all its tissues were intact, or the epidermis had been stripped off, or a thin or thick layer of the cortex had also been lost. At least four different "genera" have been founded on these different states of preservation of one and the same plant (see Chapter V. p. 131).

Among internal casts the most important examples are those which filled the medullary cavity of the Calamites or arboreal Horsetails; these casts, reproducing exactly the internal surface of the woody cylinder, constitute the most familiar remains of this group of plants, and were long confused with the stems themselves.

Seams of coal have been regarded as a case of incrustation on a great scale.[1] Here it is not single specimens, but whole masses of vegetable remains which have been incrusted by mineral matter. The remains themselves have been converted into the more or less structureless carbonaceous material which we call coal, but on the upper and lower shales we find impressions of the plants which happen to have been in contact with the adjacent mineral deposits. The coal itself has undergone great chemical changes, the organic substance having been almost entirely converted into various hydrocarbons. In certain cases, however, sufficient structure has been preserved to enable us to form some idea of the kinds of plants to which the coal owed its origin.

We now come to the other great mode of preservation, *petrifaction*, in which the whole of the organised substance has been completely saturated by mineral matter in solution, which has subsequently been precipitated in a solid form. In this case alone is the structure thoroughly preserved. There have been many petrifying agents; the two most important for us are silicic acid (H_4SiO_4), and calcium carbonate ($CaCO_3$). The most interesting vegetable remains

[1] Solms-Laubach, *l.c.* chap. i.

showing structure belong to these two classes. So far as the Carboniferous formation is concerned, silicified specimens are characteristic of the French fossil flora, while calcified remains prevail in the English coal-fields. The former have become classic through the investigations of Brongniart and Renault, the latter through those of Witham, Binney, Williamson, and others. In good specimens of both kinds, the whole microscopic structure is often preserved with marvellous perfection. It has been alleged that the French silicified specimens are the more perfect of the two, but, beautiful as they are in many cases, the calcareous petrifactions are on the whole superior to them in the preservation of structure. In the calcified specimens the actual organic substance remains, though chemically altered. The entire network of cell-walls, sometimes showing even their most delicate markings, traverses the matrix; in the cavities some remains of the cell-contents are often preserved.

The following analyses, which the authors have kindly permitted me to reproduce, are from a forthcoming paper by Miss M. C. Stopes, D.Sc., and Mr. D. M. S. Watson:—

	Seam near Bacup, Upper Foot Mine.	New Horizon at Stalybridge.	Burntisland, Lower Carboniferous.
Calcium Carbonate, $CaCO_3$	51.188	87.827	80.192
Magnesium Carbonate, $MgCO_3$	42.820	6.212	3.967
Ferrous Carbonate, $FeCO_3$	2.342	1.026	0.825
Ferric (?) Oxide, Fe_2O_3	...	...	traces
Manganous Carbonate, $MaCO_3$	0.521	0.853	1.146
Alumina, Al_2O_3	traces	traces	traces
Calcium Phosphate, $Ca_3P_2O_8$	0.525	traces	traces
Iron Pyrites, FeS_2	0.339	1.430	...
Silicate of Alumina (Clay)	0.119	0.000	10.492 [1]
Carbonaceous Matter	1.855	2.579	3.051
Free Moisture	0.264	0.100	0.305
	99.973	100.027	99.978 [2]

The carbonaceous material in these analyses is specially interesting, because it represents the actual tissue preserved in the petrifaction. In some silicious specimens, however, the organic substance has entirely perished, and the cell-walls are represented by a system of minute crevices in the matrix. Though all the essential features of the structure may be thus marked out, they may still be very difficult to see. In such cases M. Renault made use of stains, by which the cracks representing the cell-walls were injected. He thus obtained a coloured image of the structure, and so for the first time succeeded in staining a fossil

[1] Taken together with all the inorganic residues.

[2] The figures are practically percentages, according to weight. The first two columns give the analyses of "coal-balls" from the Lower Coal-measures of Lancashire. The third column relates to the plant-bearing calcareous deposit near Burntisland, in Scotland, at a much lower horizon. The most important variation is in the amount of Magnesium Carbonate, which in many of the coal-balls is nearly equal to that of the Calcium Carbonate.

section. Other substances, such as calcium sulphate and phosphate, have played a part in petrifaction, and so too, among organic products, has amber. In a few cases, fine clay has penetrated vegetable substances sufficiently to cause an effectual petrifaction; one important specimen, to which we shall have occasion to refer, is preserved in this way (see Chapter IV. p. 107).

The calcified remains of the English Coal-measures occur largely in the form of calcareous nodules or coal-balls, stony masses which are found in certain localities, especially in Yorkshire and Lancashire, in the actual productive coal-seams, and also in the "roof" above them. The former represent, as it were, parts of the raw material of coal which have been saved by petrifaction from carbonisation, and have consequently retained their structure. These nodules are literally crowded with vegetable remains of all kinds. The calcareous material, of which these nodules are formed, may have been derived from the shells of marine Mollusca, which lived and died on the old forest ground when sunk once more beneath the sea, or the lime normally contained in sea-water may have sufficed.

We can form a good idea of the sort of material which these nodules contain, if we notice the deposits of vegetable debris left on the banks of a tidal river. There we find miscellaneous fragments of plants heaped together in utter confusion, bits of reeds and rushes, rhizomes of water-lilies and aquatic grasses, twigs and scraps of bark from river-side trees, seeds, nuts, and cones. If we imagine a handful of such a conglomeration, saturated and fixed by some petrifying substance,

we shall have a very fair idea of the kind of material a coal-ball consists of.

The question whether coal was formed *in situ* in the actual forest itself, or from vegetable drift carried by currents to a distance, has been much disputed. The accumulations represented by the nodules in the coal must have been formed within the forest region, for the remains that they contain are penetrated in all directions by the rootlets of the trees which grew there. The roof-nodules, however, contain drifted fragments.

Coal-balls of this kind are limited to certain horizons, and are by no means of general occurrence, even in the Lancashire and Yorkshire district. Naturally, these stony lumps do not improve the value of the coal, and unfortunately for the palæobotanist, the mines which produce them tend to go out of working. At Shore Littleborough, in Lancashire, however, a mine has recently been reopened by the owner, Mr. W. Sutcliffe, F.G.S., for the sake of the petrifactions in which this locality is peculiarly rich.

For the purposes of the botanist, the petrified remains showing structure are the most important, and will form the main basis of our work, though it is always necessary to correlate them, as far as possible, with specimens which exhibit the external characters.

In the classification of recent plants, systematic botanists, so far at least as the Flowering Plants are concerned, are accustomed to rely chiefly on the morphology of the reproductive organs, and usually on their more external, as distinguished from their microscopic features. Such characters, however, are often absent in fossil

specimens, and it becomes necessary to make use of other means of discrimination. In the case of the Cryptogams, which play so important a part among plants of the earlier periods, few conclusions can be drawn, even where the fructifications are preserved, without the use of microscopic characters. Still more is this the case when vegetative organs alone are preserved. Among the plants of the more ancient formations, necessarily very remote from any now living, little reliance can be placed on the mere external vegetative characters, while experience has shown that anatomical structure affords a much more trustworthy clue, when interpreted with proper care and judgment. Hence the study of the more minute structure, which is beginning to take a more prominent place, even in recent taxonomy, is relatively of far greater importance when we are dealing with fossil specimens. The most favourable cases for investigation are of course those in which the fructification is itself well preserved, and, fortunately, specimens of this nature are tolerably frequent.

In selecting examples of fossil plants for our consideration, I propose to begin with the Vascular Cryptogams. It is among these plants, together with the Fern-like Spermophyta and the Gymnosperms, that palæobotany has so far made its most important contributions towards the completion of the natural system, and to these Sub-kingdoms our studies will be devoted. As we proceed we shall find that the data afforded by the study of fossil plants demand considerable modification of the current system of classification.

CHAPTER II

EQUISETALES—VEGETATIVE STRUCTURE

Calamites; Arthrodendron; Calamodendron; Protocalamites

1. *The Calamarieae.*—We know that among living Pteridophyta we can distinguish three great classes or *phyla*: the Ferns, the Lycopods, and the Horsetails. The last-mentioned group, though manifestly quite as distinct a stock as the other two, is now represented only by the single genus *Equisetum*, the species of which exhibit but small variety of structure. We might naturally suppose that in *Equisetum*, a group at once so isolated and so limited, we have the last surviving remnant of a once more extensive family. Fossil botany affords the most remarkable proofs of the truth of this hypothesis, and indeed shows that in the Carboniferous period the Horsetail stock was among the best-represented divisions of the Vegetable Kingdom. In fact, we may safely say that any adequate knowledge of the Equisetales must be derived to a much greater extent from the study of the extinct forms than from that of the few surviving representatives. In saying this, I am assuming that all the Palæozoic plants known as Calamaricae were of

Equisetaceous affinities. Though at one time some botanists hesitated to accept this conclusion, we shall find that it is now supported by irresistible evidence. It is a matter of indifference whether, with Zeiller, we name the whole group *Equisetineae*, after its sole living representatives, or term it, with Endlicher, *Calamarieae*, after its more important fossil members. The form Equisetales will be adopted in this book, as indicating a group of higher than ordinal rank.

Many of the Calamariеae attained the dimensions of trees. It is not possible to give the complete measurements of any specimen, but the following facts may afford some indication of the size attained. Mr. G. Wild found in the roof of a coal-mine in Lancashire a medullary cast of a Calamite 30 feet long; the diameter of the pith amounted to about 6 inches in the thickest part. This cast must have represented a portion only of the main trunk. In some of M. Grand'Eury's specimens the cast of the pith is over a foot in diameter; if the whole tree were in proportion, it must have been of an immense size. In other specimens of his, a height of 9 feet from the base scarcely takes us above the region where the roots are given off. M. Grand'Eury estimates the height of the stem in many of these Calamarian trees at from 20 to 30 metres.[1]

As already mentioned, the most common mode of preservation of Calamites is in the form of casts of the medullary cavity (see Figs. 2 and 3). The marks which they show correspond, not to any features of the external surface, but to the print of the inner

[1] *Flore carbonifère du Département de la Loire*, 1878, p. 29; *Bassin houiller du Gard*, 1890, p. 210.

surface of the wood. Hence the superficial resemblance of these specimens to the ribbed stem of an *Equisetum* is fallacious, except that in both cases the marks on the surface are related to the course of the vascular bundles. In some specimens the tissue of the stem surrounding the medullary cast is preserved, and the true cortical surface shown. The latter is either smooth, or, if ribbed, the ribs do not correspond to those of the

FIG. 2.—*Calamites Suckowii.* Medullary cast, showing three nodes, on one of which the cast of a branch is borne. Below each node, and between the furrows, the prints of the infranodal canals are seen. About $\frac{2}{3}$ of natural size. After Stur.

medullary casts.[1] The characters which first suggested Equisetaceous affinities having proved to a certain extent deceptive, the whole question had to be reconsidered, and the systematic position of these fossils has now been determined by arguments of quite a different kind, drawn from the fructifications and from the anatomy of specimens with their structure preserved.

[1] The external surface of the *wood*, however, in decorticated pertrified specimens, is sometimes ribbed, and may bear a deceptive resemblance to that of a medullary cast.

The most conspicuous markings on a Calamitean cast consist of longitudinal ridges and furrows, the former usually broader than the latter. The specimens are

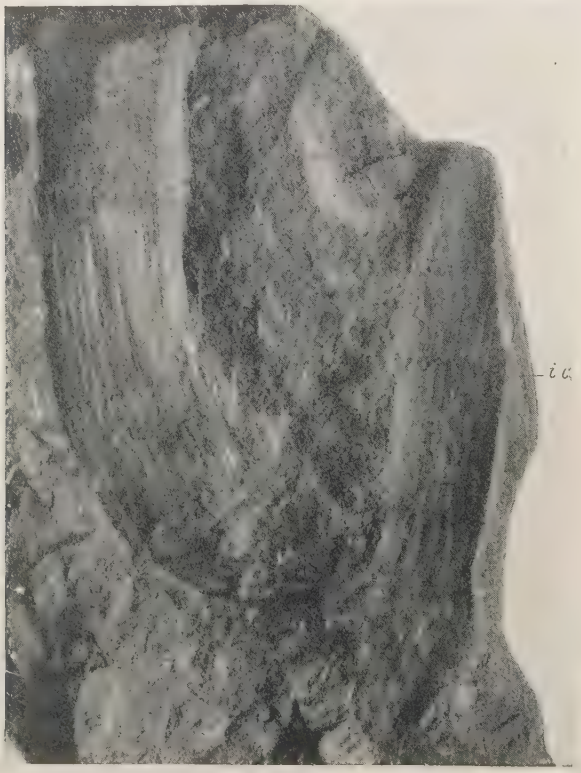

FIG. 3.—*Calamites Suckowii.* Medullary cast, bearing the cast of a branch larger than that of the main stem. *i.c.*, the prints of the infranodal canals below a node. ¾ of natural size. From a photograph by Mr. R. Kidston, F.R.S.E., taken from a specimen in his collection, found at the Oaks Colliery, Barnsley; Middle Coal-measures.

distinctly jointed, the joints being marked by zigzag commissural furrows. It has always been recognised that these joints represent the nodes. Often, but not in-

variably, the ridges and furrows of successive internodes are alternate with one another. Many of the specimens taper towards one end, which, as we shall subsequently show, corresponds to the base of the branch (see Fig. 2). Above the nodes we often find more or less circular scars, of relatively large size, which there is reason to believe mark the position of the lateral branches. In well-preserved casts it is usual to find a small circular or elliptical elevation on the surface of each ridge, just below the node (see Fig. 2, Fig. 3, *i.c.*). In most of these fossils the tissue of the stem enclosing the cast has become reduced to a comparatively thin coaly rind. In a few cases the anatomical structure of the wood and the cast of the pith are preserved in the same stem,[1] and such specimens afford the best evidence for the identification of the two classes of remains. We will defer a full explanation of the markings on the cast until we have considered the anatomical structure.

2. *The Stem of Calamites.*—Petrified specimens of the various parts of plants belonging to the Calamarieae are common in the calcareous nodules of the Lower Coal-measures of Britain and among the silicious remains in the Upper Coal-measures and Permian of France, as well as at other horizons. The anatomical structure of all the organs has thus become known, though the correlation of the fragmentary remains has presented great difficulties.

We will now go on at once to the anatomical description of the first type to be considered in detail,

[1] See, for example, Williamson, "Organisation of the Fossil Plants of the Coal-measures," Part i., *Phil. Trans. Roy. Soc.* 1871, Plate xxvi. Fig. 21.

namely the genus *Calamites*. Included in this group there are many so-called species, though they are very difficult of distinction. As to the sense in which the name *Calamites* is used here, the characteristics of the genus will become evident as we go on, and I will only mention now that *Calamites*, as the name is employed in the present book, is equivalent to the *Arthropitys* of many palæobotanists, especially in France.

If we examine, by means of sections, the ordinary form of stem of a typical Calamite in the petrified condition, with well-preserved structure, we find the following characters: the pith is generally hollow, only its outer zone being preserved, and the definite internal limit which we often find to this persistent zone, leads us to believe that the pith was fistular during life, and that the cavity is not merely the result of decay. In Fig. 4 part of a transverse section of a Calamitean stem is shown. The pith, as usual, was hollow, but only the persistent layers of the external part are represented. Around the pith is a ring of collateral vascular bundles; here, as in the great majority of specimens, a considerable mass of secondary tissue has already been formed, so that each of the bundles has assumed a more or less regular wedge-like form. On the inner limit of each, we find, with the rarest exceptions, a definite canal, so that the whole appearance recalls very much that of a section of the stem of one of the living *Equiseta*. The question whether this appearance indicates a real identity of structure is one which we shall have to consider presently. In most specimens everything outside the

wood has perished, but in a minority the cortex is preserved (see Fig. 4).

We will defer for the moment the consideration of the wood, which we will take more in detail afterwards, and pass on to the cortex. This consists of two zones, the inner formed of a rather thin-walled tissue, some cells in which contain very dense black carbonaceous

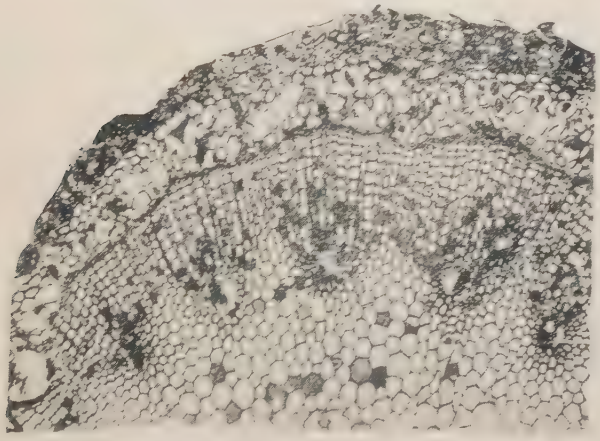

FIG. 4. *Calamites*, sp. Part of transverse section of a young stem, showing pith, cortex, and five vascular bundles, each with a canal at its inner edge. In some of the canals remains of the spiral tracheides can be seen. Beyond the secondary wood, and next the cortex, are traces of the phloëm. × about 40. From a photograph by Prof. J. B. Farmer. Will. Coll. 1553.

matter, and have been supposed to represent secretory organs, while the outer zone consists of smaller cells, with thicker walls. In some exceptional cases we find in this zone regular fibrous ribs alternating with parenchymatous bands. In fact, we have, in such specimens, very much the same mechanical arrangement as we find in the stems of recent Equisetaceae. In a few instances we have been so fortunate as to find stems

preserved at the very commencement, or even before the commencement, of secondary growth, as shown in Fig. 5. This is a comparatively rare stage to find, and when it is found, it is nearly always in a small twig. The larger stems of *Calamites* are rarely, if ever, met with at so early a stage of development. In a twig in this early condition, before secondary thickening has begun, the pith is often persistent (though fistular in the specimen figured), and round it we find a ring of

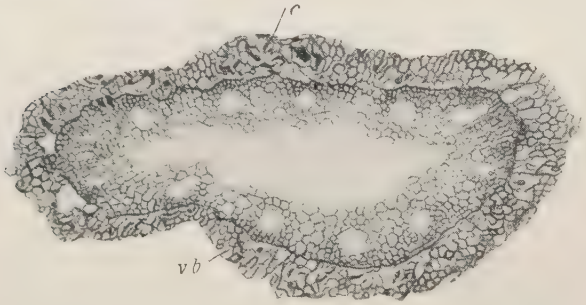

FIG. 5.—*Calamites*, sp. Transverse section of a very young twig, showing primary structure. *c*, cortex; *vb*, vascular bundles, of which there are twelve, each with its canal. × nearly 40. *Phil. Trans.*, W. and S. Will. Coll. 1561.

primary vascular bundles, in which the wood is but little developed, and then the cortex. The whole structure is strikingly like that of the stem of an *Equisetum*.[1] Now one of the most important questions to be settled, bearing on the comparison with recent Equisetaceae, is this: Are these canals in *Calamites* really homologous with the carinal canals of an *Equisetum*, or are they of a different nature, perhaps, as some observers formerly thought, representing the phloëm?

It has been observed that, in many cases, in the

[1] Cp. Scott, *Structural Botany*, Part II. Fig. 39, showing the transverse section of a small stem of *Equisetum arvense*.

transverse section of a stem, the canals are not perfectly empty, but that they contain minute rings adhering to their edges, as indicated in Fig. 4. This suggests very strongly the position of the annular and spiral tracheides in *Equisetum*, which are often found within the carinal canal. To determine the true state of the case, however, a very detailed examination was necessary. There are now many sections showing these canals quite clearly, and proving that they contain the first-formed woody elements, or protoxylem, of the vascular bundles.

FIG. 6.—*Calamites*, sp. Part of radial section through primary wood. *px*, disorganised spiral and annular tracheides in the canal; *sc*, scalariform tracheides of the more external primary wood. On the left is the pith. × about 160. *Phil. Trans.* W. and S. Will. Coll. 20 A.

Fig. 6 represents a radial section passing through the canal of one of the bundles. On the inner side of the canal is pith; on the outer side wood. We notice that the canal is to a great extent occupied by the disorganised tracheae. It is a point of some importance that the disorganisation is found to be greatest on the inner side of the canal, while, as we approach its outer edge, the tracheae become more continuous. We know that the disorganisation of the tracheae is constantly greatest in that part of the primary wood which is differentiated before the growth in length is completed. Hence we may infer that the

innermost elements, being the most disorganised, were the earliest formed ; and we thus obtain a proof that the development of the primary wood was strictly centrifugal.

The elements of the primary wood, other than those in the canal, present no special interest. We find the spiral and annular tracheae of the protoxylem replaced by other elements (scalariform or pitted) as we get beyond the canal. I have spoken of these bundles as collateral. In the very best preparations, we can satisfy ourselves that on the inner side of the vascular bundle there are no traces of phloëm ; the canal abuts directly on the pith. On the other hand, in very fortunate cases, where the preservation is exceptionally good, we find, on the outer side of the wood, strands of delicate tissue made up of small thin-walled elements ; these we can only interpret as phloëm-groups ; we find, further, between these groups and the wood, remnants of cells of the cambium itself. Some traces of these tissues will be recognised in Fig. 4, immediately outside the secondary wood.[1]

We thus see that the structure of the young stem of a Calamite is in all essentials similar to that of an Equisetaceous stem. Surrounding the usually fistular pith, interrupted at every node by a persistent diaphragm (see Fig. 7), we have a ring of collateral vascular bundles, with centrifugally developed wood ; at the inner border of each is a canal containing the disorganised tracheae of the protoxylem.[2] Thus, the Calamite, so

[1] For special figures of the phloëm and cambium, see Williamson and Scott, "Further Observations on the Organisation of the Fossil Plants of the Coal-measures," *Phil. Trans.* vol. 185, B, 1894, Plate lxxviii. Figs. 12-14.

[2] In a Calamarian stem of Lower Carboniferous age, from the Burntisland

far as anatomy goes, is simply an *Equisetum* with secondary thickening. In order to carry the comparison further, we must settle one or two points, especially the course of the vascular bundles. In *Equisetum* itself their course is exceedingly simple: a single vascular bundle enters the stem from each leaf, and

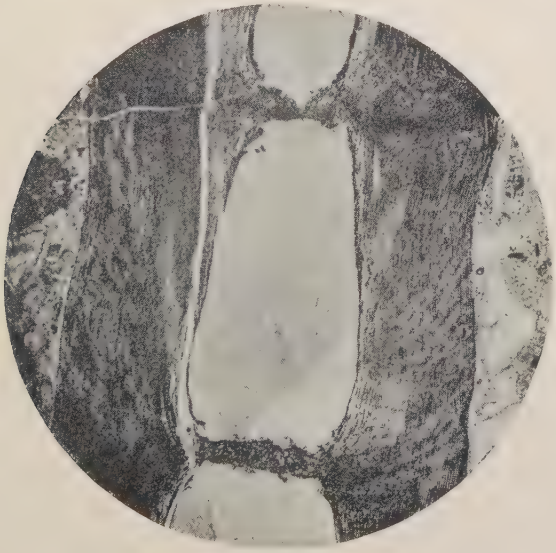

Fig. 7.—*Calamites*, sp. Radial section of a decorticated stem, with fairly thick wood, showing the fistular pith, crossed by diaphragms at the nodes. × 9. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 1937.

passes straight down through one internode only. At the node next below, the bundle forks, and its branches attach themselves to the adjacent alternating vascular bundles passing out at that node. This type is often

deposits, named provisionally *C. pettycurensis*, groups of centripetally developed wood are present on the inner side of the canals. This is a point of interest, as tending to connect the Calamarieae with the Sphenophyllales, in which the primary wood is centripetal (see pp. 36 and 89).

found in the Calamites also, but on the whole, the bundle-system of the latter is less regular and more complicated. Sometimes the bundles of successive internodes are not alternate, but run on in the same straight line. Where this is the case, the forks of the bundle, as we trace it down, instead of attaching themselves to the alternate bundles at the node below, converge again on the other side of the outgoing leaf-trace, so as to form a loop, through which the trace passes out, and the bundle below the loop continues in the same straight line as before. This straight course of the bundles and absence of alternation between those of successive internodes, is specially characteristic of one very ancient type of the Calamaricae, namely the genus *Bornia* or *Archaeocalamites*, which occurs in the Lower Carboniferous and the Devonian formation (see p. 70).

Secondly, we may find a greater complexity in the vascular system. In this case the bundle may run down through more than one internode, and pass on to the second node below (Fig. 8). It follows that here the number of vascular bundles in each internode may be double that of the leaves in a whorl. Where a bundle passes between the outgoing traces at the node, it may either be connected with them by lateral strands or remain free. The former case is illustrated by Fig. 8, from a large and perfectly preserved stem. We may therefore express the general characteristics of the Calamarian vascular system by the statement that the whole arrangement is of the type of *Equisetum*, but more varied, and sometimes more complex. I may further mention that these variations may even occur

side by side in different parts of one and the same specimen.

The following considerations serve to identify the leaf-traces. We constantly find in all specimens of *Calamites*, that at every joint a whorl of small and

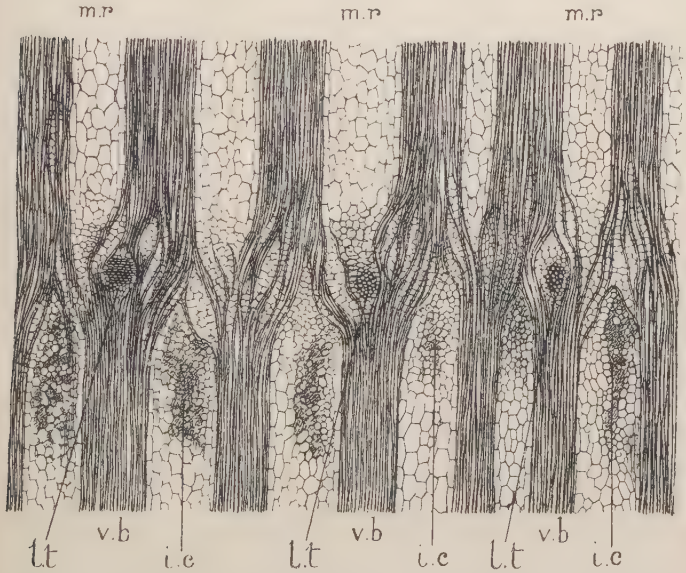

FIG. 8.—*Calamites communis.* Tangential section of wood, passing through a node, and cut near the pith. *v.b.*, Vascular bundles of the stem. *l.t.*, leaf-traces cut transversely as they turn outward at the node. Note that they are only half as numerous as the bundles of the stem. *m.r.*, primary medullary rays. *i.c.*, small-celled tissue of the rays below the node, corresponding to Williamson's "infranodal canals." × 12. S. Coll. 897. (G. T. G.)

uniform bundles passes out, and though it is only in the very rarest cases that we are able to trace out these bundles continuously into the leaf, yet there is no doubt that these outgoing bundles are really the leaf-traces. For one thing, their arrangement precisely corresponds with the arrangement of the leaves, as

shown in certain specimens which have retained their foliage, and we know that each of these whorled leaves actually received a single bundle from the stem (see Fig. 12). Secondly, the outgoing bundles form the direct continuation of those which traverse the internode below, precisely as is the case with the leaf-traces of *Equisetum*. And then again we have the argument of exclusion. If these bundles are not leaf-traces, what are they? They must in that case be either traces of branches or of roots. But as we shall see below, the connection of these organs with the stem is now well known, and is quite independent of the bundles in question. By all these considerations the interpretation of these outgoing bundles as leaf-traces is now fully established. If a section be cut tangentially through the wood, it intersects these bundles transversely (see Figs. 8 and 9). They also appear (cut longitudinally) in the transverse sections of the stem, which pass exactly through a node. A radical section in the plane of the outgoing strand shows that the primary bundle passes out as a whole on its way to the leaf, and can be followed through the secondary wood. The whole course of the leaf-traces is thus made clear from every point of view.[1]

The next point to be considered is the structure of the secondary wood. We find that the wood as a whole is divided up into the bundles, and the principal rays between them. The behaviour of these rays in passing through the wood is a matter of some importance, for great emphasis has been laid on it in discriminating

[1] For further illustrations of all these points, see the memoir by Williamson and Scott, above cited.

species. It is obviously desirable to aim at establishing species on anatomical lines, and if possible to correlate them with the various forms of casts. A great many attempts have been made in that direction, but at present with imperfect success. We find, however, the following variations, whatever may be their taxonomic value. In comparatively few cases we can trace the ray in undiminished width throughout the whole thickness of the wood. That seems to be the characteristic of the type which the French authorities call *Arthropitys bistriata*, a form of *Calamites*. Then we may have the opposite extreme; the ray may come to an end almost immediately, and thus be shut off by interfascicular wood; or, again, it may gradually die out, becoming encroached upon laterally by the wood, and cut up by strands of intercalated tracheae. This last is the commonest form among English Calamites (*Calamites communis*, Binney). It is not very easy to determine how this mode of enclosing a ray by the wood was brought about, because the tracheae are very long and the ray-cells which they replace very short, and yet the radial arrangement of the elements is not disturbed. The only explanation appears to be that the growth must have taken place in the cambial cells themselves, rather than in their products.

I have hitherto spoken of tracheae, using the word in its widest sense, so as to leave open the question as to the true nature of the woody elements. First of all, were they tracheides, derived from single cells, or vessels, arising by cell-fusion? We constantly find that they have tapering ends, with no evidence of perforation; but there is this difficulty, that every now and then

there are distinct traces of transverse walls in these elements. This, however, is very inconstant, and where these apparent transverse walls appear, they seem to be perfect septa, and not merely annular ridges such as we are accustomed to find in vessels, marking the limits of their constituent cells. I am disposed to think that the elements of the wood in *Calamites* were occasionally septate, unlike true tracheides, but there is no proof that they ever arose by cell-fusion, and we cannot therefore regard them as vessels in De Bary's sense. There is evidence that the pits, which were either scalariform or of the rounder, multiseriate type, were closed.

The disposition of the pits is of some interest. Throughout the whole of the secondary wood they are limited to the radial walls. The general arrangement was thus very much like that in the Coniferae of the present day, and the mechanism of water-conduction must have been similar. The cells of the medullary rays have this peculiarity, that they are generally longer vertically than in any other direction, and thus the rays have not the muriform appearance which is general, though not universal, among recent plants. Some of the rays are very small, and may even consist of a single radial row of cells.

I have already given the principal facts about the primary cortex. In the few cases in which we find the cortex well preserved in an old stem, there is an enormous development of periderm, as shown by a specimen in the Williamson Collection, which has secondary wood two inches thick, and bark of even greater thickness.[1]

[1] Figured in Williamson, "Organisation of Fossil Plants of the Coal-

Occasionally, in comparatively young stems, we find tangential divisions beginning in the inner cells of the cortex, and it is highly probable that this was the first commencement of the periderm-formation which attained such a great extent in the older stems. The trunks of the larger Calamites must have had a regular bark, like that of our forest-trees, but thicker than in most of the latter.

3. *Branching.*—The next question to be considered is that of the branching of the stem. It is very common to find the bases of branches in connection with the main axis. The section represented in Fig. 9 is a tangential one, passing through the base of a branch, where it joins the primary wood, so that its tissues are shown in continuity with those of the stem which bears it. The insertion of these branches is very regular. They are always placed immediately above the node, and usually between two of the outgoing leaf-trace bundles (Fig. 9). Sometimes a branch may be nearly or quite as large as the main stem, repeating all the characteristics of the latter; in other cases we find lateral branches which are very small in comparison with the main stem;[1] such lateral shoots often occur in considerable numbers in a verticil. It is an interesting point that these little branches were in many cases abortive, as shown by the fact that we often find their bases completely enclosed in the wood. At the same time that this was proved for the English specimens, Renault

measures," Part ix., *Phil. Trans.* 1878, Part ii. Plate xx. Figs. 14 and 15; also in Seward's *Fossil Plants*, vol. i. Fig. 78.

[1] The medullary casts shown in Figs. 2 and 3 illustrate these two cases.

came to exactly the same conclusion independently, from the study of the French material. These observations show that very often the small lateral branches

FIG. 9.—*Calamites communis.* Tangential section of wood, passing through a node, as in Fig. 8, but showing the base of a branch, inserted between and above two of the leaf-trace bundles. *f*, vascular bundles of stem; *m*, leaf-traces; *c*, medullary rays. × 20. After Williamson, *Phil. Trans.* Will. Coll. 90.

were cast off early, a fact which admits of two explanations. The branch may either have been abortive altogether, or, which is still more likely, it may have been caducous, forming a limited shoot of temporary duration,

comparable to the spurs which bear the needles in *Pinus*.

The position of the branches with reference to the nodes and leaf-traces was precisely the same in *Calamites* as in the recent *Equisetum*. The pith of the branch tapered towards the point of attachment, so that its actual junction with the pith of the main stem was effected by a slender neck of tissue. This fact is shown quite clearly by sections of specimens passing through the junction of stem and branch, and explains one of the most characteristic forms of Calamitean casts, which in a great many cases are tapered towards one end. Figs. 2 and 3 each show the medullary cast of a branch in connection with that of the stem, and confirm the evidence, derived from sections, that the pith became gradually smaller towards the point of attachment. Some of the older observers thought that the tapered end was the apex, thus turning the specimen wrong way upwards.[1] The root-bearing base of the main stem was also tapered.

4. *Other Types of Stem.*—The type which I have been describing so far is, as I have already said, the *Arthropitys* of the French authors, and this is the least complex of the Calamarian stems. We have seen that the structure of the wood is, after all, very simple. It consists essentially of the tracheae and the medullary rays—including both primary and secondary rays. The differentiation is about on a level with

[1] The proof that the pith tapers towards the base of the branch has enabled us to determine with certainty the upper and lower ends of specimens, a point otherwise by no means easy of decision.

that of the simplest Coniferous woods of the present day, as, for example, that of the Yew.

There are certain other Calamarian types of stem-structure, some of which have long been distinguished. There is one form which became known to us by the observations of Williamson, who founded a new genus for it under the name of *Calamopitys*, but he afterwards let the generic distinction drop, although the type is quite distinct from the ordinary Calamitean structure already explained. The name *Calamopitys* is not admissible, as it had previously been employed by Unger in a different sense,[1] and that of *Arthrodendron* has now been substituted. The *Arthrodendron* type of stem is a rare one. The wood, in the specimens known, is of no great thickness, and the primary bundles are widely separated by the principal medullary rays. The chief peculiarity is in the structure of the rays, which are formed, for the most part, of vertically elongated prosenchymatous cells, thus differing widely from the usual parenchymatous structure of these organs; but within these primary rays are little secondary rays of parenchyma, like those of the true wood. *Arthrodendron* has also some other peculiarities, but the complex rays suffice to mark it off from the ordinary Calamites.

There is another important type, not represented in England—that of *Calamodendron*,—which is the most complex of all (see Fig. 10). Here each of the principal rays consists of a middle band of parenchyma, more or less like an ordinary medullary ray, and on either side of this, separating it from the wood, is a broad band of fibrous prosenchyma, in which secondary rays occur.

[1] See Chapter XI.

In fact, the principal rays are here much more complex in structure than the wood itself. The *Calamodendron* stems are especially characteristic of the Upper Coal-measures and Permian of Central France.

This brings us to the question of nomenclature, on which I must say a word. Brongniart, in his earlier works, placed all the Calamitean stems then known to

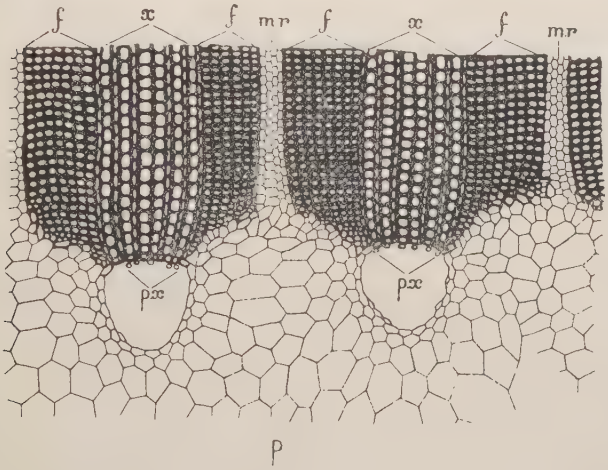

FIG. 10.—*Calamodendron intermedium*. Part of transverse section of stem, showing inner portions of two vascular bundles, with secondary wood. *p*, pith; *px*, protoxylem in canals of the bundles; *x*, fascicular wood, containing secondary rays; *f*, prosenchymatous parts of principal medullary rays; *mr*, central parenchymatous portion of each ray. Magnified. After Renault.

him in the one genus *Calamites*, and believed them to be related to the Equisetaceae; subsequently he investigated specimens with the internal structure preserved, and in all clear cases of the kind he found a well-developed secondary wood. Wherever he found this, he thought he must have to do with a Dicotyledonous flowering plant of Gymnospermous affinities, for in those days Gymnosperms were usually included

under Dicotyledons. Consequently, Brongniart was led to divide the Calamites into two groups: those which he supposed had no secondary growth, and which he therefore left under the old generic name of *Calamites*; and those which had such growth. The latter he transferred to Phanerogams, founding the genus *Calamodendron* for their reception.[1] *Calamodendron* was subsequently subdivided by Göppert into *Arthropitys*, with simple medullary rays, and *Calamodendron* proper, with the more complex structure which I have just described.

There is at present no evidence remaining that any Calamarian plant was without secondary growth. The Calamites supposed to be without secondary thickening have turned out to be simply medullary casts, from which the surrounding tissues have partly or wholly perished. The specimens with their structure preserved invariably possess secondary tissues, the only exceptions being excessively young twigs, and even these often show the commencement of the cambial growth (see Fig. 5). At present the evidence is that all Calamites, so far as they are known to us, formed secondary wood and bast, and consequently this distinction of Brongniart's falls to the ground. We may therefore go back to the old name *Calamites*, using it as synonymous with the *Arthropitys* of the French authors, and retaining the genus *Calamodendron* in Göppert's restricted sense.

Another type of Calamarian stem is represented by *Calamites pettycurensis*, already referred to (p. 24). It

[1] See Brongniart, *Tableau des genres de végétaux fossiles*, Paris, 1849, pp. 47-50. Brongniart was also influenced by the occurrence of seeds among the branches of *Asterophyllites*, which he regarded as the foliage of *Calamodendron*.

is interesting that this Lower Carboniferous species should be the only Calamite so far observed which has centripetal wood. The protoxylem is in the usual position, in or adjacent to the "carinal" canal, but in this case the development of the primary xylem proceeded in both the inward and outward directions, for each bundle possesses a considerable arc of centripetal

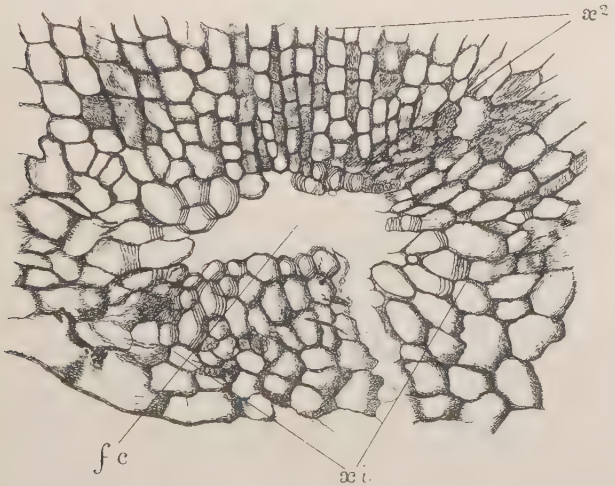

FIG. 11.—*Calamites* (*Protocalamites*) *pettycurensis*. Transverse section of the xylem of a vascular bundle in the stem. *fc*, fascicular canal; x^2, secondary wood; *xi*, centripetal wood, on the inner side of the canal. × about 140. S. Coll. 1104. (G. T. G.)

wood on the side of the canal towards the pith (Fig. 11, *xi*). Dr. Lotsy has suggested to me that a new genus or subgenus, *Protocalamites*, should be founded on this form, and the proposal may be provisionally adopted, but it is possible that when the course of the bundles has been traced the species may prove to belong to *Archaeocalamites* (p. 70). The significance of the centripetal xylem as a character shared with other

classes of Pteridophyta will be emphasised in later chapters.

5. *The Leaves.*—The leaves of the Calamarieae were in all cases arranged in whorls, and were usually of a simple acicular or lanceolate form, though in the genus *Archaeocalamites* they were forked (Figs. 30, 31). It is often stated that the leaves of the Palæozoic Equisetales differed from those of their later successors in being

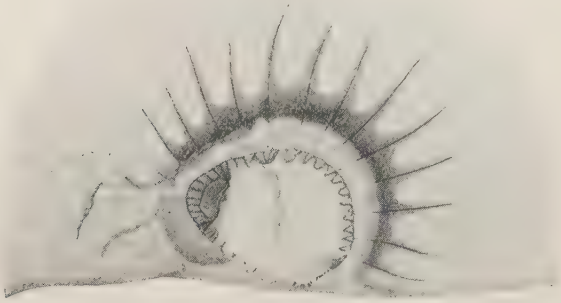

Fig. 12.—*Calamites*, sp. Transverse fracture through a node, showing leaf-sheath and free tips of leaves, each with its vein. Commissural bundles also shown. × about 2. From a specimen in the possession of Mr. Parker of Rochdale. (G. T. G.)

free, and not united to form a sheath. It is no doubt true that the free laminae were much more developed in the Calamarieae than in recent Horsetails, but in several cases there is good evidence for the presence of a coherent sheath at the base. This is clearly shown in Fig. 12, which represents the node of a Calamite, exposed in transverse fracture on the surface of the matrix. The greater part of the whorl of leaves is shown, and they are evidently united into a continuous

sheath at the base. Each leaf is traversed by a vein, and further to the interior the commissural vascular bundles of the node are visible. It is possible that in many cases the sheath became split up as the stem increased in thickness.

Immediately below a node the cortex of the stem shows in some specimens a number of prominent ribs, corresponding to the bases of the verticillate leaves

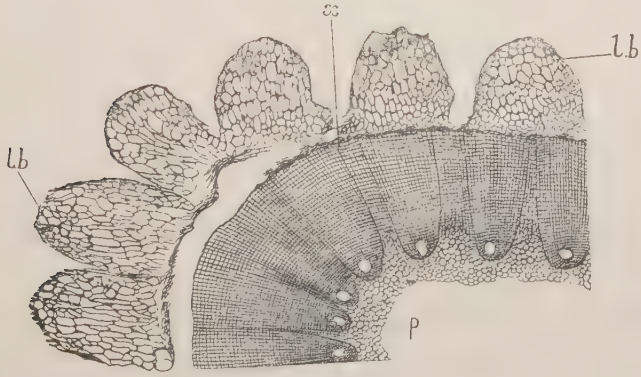

FIG. 13.—*Calamites*, sp. Part of transverse section close to a node, showing the prominent leaf-bases, *l.b.* *x*, secondary wood ; *p*, fistular pith. Magnified. From a section lent by the late Mr. J. Butterworth of Shaw. (G. T. G.)

which sprang from the node. This is well shown, in transverse section, in Fig. 13.[1]

As regards the anatomical structure of the leaves of the Calamites there is comparatively little to be said. In *Calamites* itself the simple acicular leaves were each traversed by a single nerve (see Fig. 12); in some of the other forms, as in *Calamocladus*,[2] according to

[1] For the use of the specimens illustrated in Figs. 12 and 13 I am indebted to the late Mr. John Butterworth of Shaw.

[2] The foliage of Calamarieae will be further described, as regards its outward aspect, in the following chapter.

Grand'Eury, they appear to have had several parallel nerves, but nothing is known as to the internal structure of these specimens. The late Mr. Hick of Manchester[1] published an interesting paper on the structure of the leaves of *Calamites*, in which he gave a full account of the anatomy of the small leaves which

FIG. 14.—*Calamites*, sp. Transverse section of a bud at the apex of a small twig, showing axis, with parts of two whorls of leaves. L, a leaf of outer verticil; L', leaf of inner verticil, in connection with stem. × 30. S. Coll. 171. (G. T. G.)

were borne on the most minute twigs. In various cases the axis bearing these appendages clearly shows the structure of *Calamites*. We know, from the evidence of impressions, that leaves of much larger dimensions were borne on the stems and more considerable

[1] *Mem. and Proc. Manchester Lit. and Phil. Soc.* ser. iv. vol. ix. p. 179, 1895.

branches; the larger leaves, however, are practically unknown in the petrified condition. In Fig. 14 a tranverse section of a bud, showing a number of the leaves arranged in whorls around the axis, is represented. They have the same form in transverse section as *Pinus* leaves. In the middle there is a collateral vascular bundle, usually with the wood alone preserved. The bundle is surrounded by a pericycle of thin-walled parenchyma, and outside this we find a sheath of large cells containing carbonaceous matter, perhaps derived from some product of secretion. Long cells, radiating out from the central cylinder, form a definite palisade-tissue, presumably the assimilating layer; at the periphery is an epidermis, in which the stomata are sometimes clearly shown. This is a perfectly simple and straightforward type of leaf, and it is sometimes very well preserved. There is thus no difficulty as regards the structure, in the case of the leaves, of very small size, which were borne on the slender twigs of Calamites. There is a great resemblance between the vegetative leaves and the bracts of Calamarian cones.

6. *The Roots.*—As regards the roots of Calamarieae, we are now in possession of a considerable stock of information. In Williamson's paper of 1871—the first of his Royal Society series—among the varieties of *Calamites* the author described some specimens which differed from the ordinary form, for they had a solid pith and no fascicular canals. In a later memoir he distinguished organs of this type under the generic name of *Astromyelon.* In the meantime Messrs. Cash and Hick had found some beautiful specimens with the

cortex preserved, which they named *Myriophylloides*. These also were referred by Williamson to his genus *Astromyelon*.

The following are the chief characters of *Astromyelon*: it has often a persistent pith, though, in the larger specimens, it may have become fistular in the middle. In the specimens first described the pith is of relatively large size. It is surrounded by a ring of bundles, and we shall find there is good evidence that the development of their primary wood was centripetal, not centrifugal as in the stem. In almost all the specimens a thick zone of secondary wood is present. Most often the wood is decorticated, but when the cortex is present it has a very lacunar structure, containing a ring of large intercellular spaces. It is only in very good specimens that the phloëm is preserved (see Fig. 15).

Now some of the smaller specimens, which used to be included in the *Myriophylloides* of Hick and Cash, have a very different structure from those just described. Some of them have no pith, and the groups of primary wood are very few in number (see Fig. 16). The structure of the cortex, however, is the same in all, and the extreme types are connected by a series of intermediate forms.

Renault, in 1885, expressed his conviction that the French specimens, which he recognised as agreeing with Williamson's genus, were the roots of *Calamites* (his *Arthropitys*) and of *Calamodendron*, and he made out a strong case for his belief.[1] His suggestion, however,

[1] Renault, "Nouvelles Recherches sur le genre *Astromyelon*," *Mem. Soc. Sci. Nat. de Saône et Loire*, 1885.

was not at once accepted, because he had not obtained the evidence of actual continuity at that time. Later

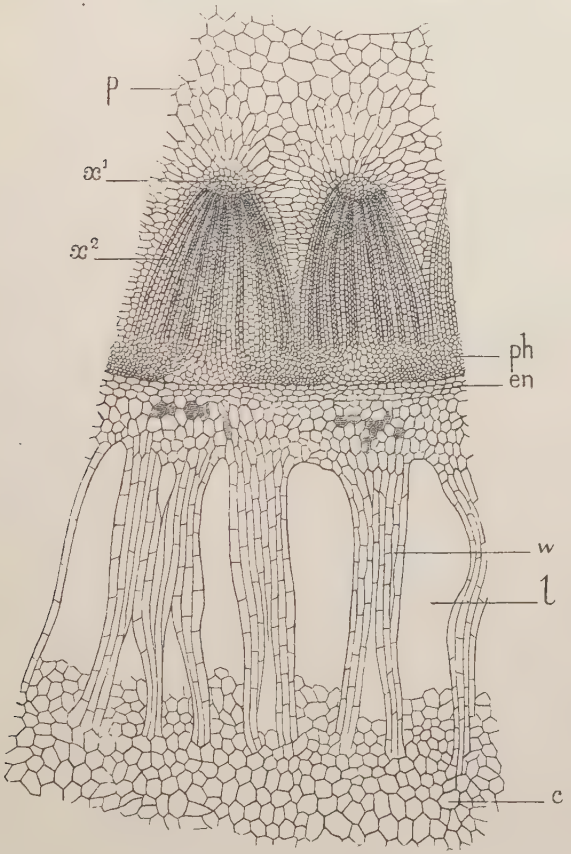

FIG. 15.—*Calamites*, sp. Part of transverse section of a large root. *p*, pith; x^1, primary centripetal xylem; x^2, secondary xylem; *ph*, phloëm; *en*, endodermis; *l*, lacunae of cortex; *w*, cellular walls separating them; *c*, outer cortex. Magnified. After Renault.

on—in 1893—Renault described certain beautiful specimens of Calamites, which afforded the proof required, for in them the Calamitean stem bears

appendages in which the typical *Astromyelon* structure is evident.[1] This evidence proved quite conclusively that *Astromyelon* was only an appendage of the stem of *Calamites*. Since then the connection between the two organs has also been clearly demonstrated in various specimens from the English Coal-measures.

The relation between the roots and the stem has recently been fully investigated by Mr. Maslen,[2] who finds that the roots, like the branches, were commonly inserted on the node, between two of the outgoing leaf-traces (cf. Fig. 9); the roots, however, arise on a level with the leaf-traces, and not above them, and pursue a somewhat downwardly directed course in passing through the wood of the main axis.

The question whether these appendages were roots or branches had to be decided from the anatomy. In the first place, as already mentioned, the primary xylem was centripetally developed. On the inner side of each woody wedge we find in transverse section a little triangular group of tracheae, and this triangular group has always the smaller elements towards the exterior (see Fig. 15, x^1). Radial sections prove that these external elements of the primary wood are spiral tracheae, and thus the position of the protoxylem is shown to be that characteristic of roots.

Another point of crucial importance is the arrangement of the primary xylem and phloëm groups; it is not often that such a point as this can be demonstrated in a fossil. We were able, in one or two favourable

[1] *Flore fossile du Bassin houiller d'Autun et d'Epinac*, Part ii. p. 106, Plate lii. etc.

[2] A. J. Maslen, "Relation of Root to Stem in Calamites," *Annals of Botany*, vol. xix. 1905, p. 61.

cases, to trace the centripetal strands of xylem in a young root, and to find, alternating with them, groups of delicate tissue, which could only be interpreted as primary phloëm. Hence, in this respect also, the structure proves to be that of a typical root.

We further found that the bases of branches of *Astromyelon* are surrounded by a distinct cortex of their own, as they traverse the outer tissues of the parent organ. Hence they must have been endogenous in origin, thus agreeing with rootlets. Another important point is the entire absence of anything like nodes.

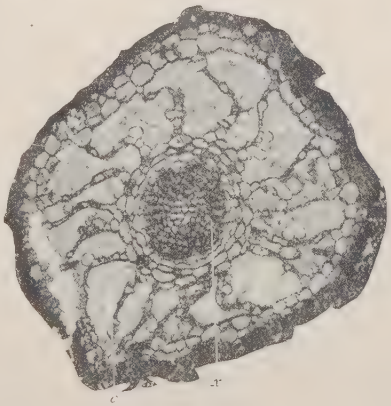

FIG. 16.—*Calamites*, sp. Transverse section of small tetrarch rootlet, showing wood (*x*), with slight secondary growth, double endodermis, lacunar cortex (*c*), and thickened exodermis. × 25. From a photograph. *Phil. Trans.* W. and S. Will. Coll. 1890, A.

There is thus, on the whole of the evidence, no room for doubt that the old genus "*Astromyelon*" simply represents the roots and rootlets of *Calamites*.[1] Other allied forms appear to stand in a similar relation to *Archaeocalamites* and *Calamodendron*.

The endodermis was evidently double, as in the roots of recent Horsetails; this is well shown in the small tetrarch rootlet represented in Fig. 16. The large intercellular spaces of the cortex were no doubt an adaptation for growth under water, or in wet mud.

[1] Williamson and Scott, "Further Observations, etc.," Part ii. The Roots of *Calamites*, *Phil. Trans.* vol. 186, B, 1895.

The cortex is bounded externally by a layer of cells with very thick outer walls, comparable to the exodermis of many recent roots (Fig. 16). In the older roots a periderm was formed, the external cells of which, as Dr. M. C. Stopes has shown, thickened their outer walls and replaced the primary protective layer.

We have now obtained a fairly good idea of the whole construction of a Calamarian plant, as regards its vegetative organs. We have a thorough knowledge of the structure of the stem in various types, and though much has still to be learnt about the comparative anatomy of the leaves, we now know almost the whole story of the structure of the roots and branches, and their relation to the stem.

7. *The Medullary Casts.*—One thing remains to be said before leaving the vegetative organs, in order to complete the anatomical explanation of the markings on the casts. We have already seen, as shown in the first illustrations to this chapter, that every Calamitean cast shows longitudinal ridges and furrows. It is quite evident that the furrows on the cast correspond to the vascular bundles. We have to imagine the soft tissues decayed, leaving only the woody tissues behind, so that each wedge-shaped strand of wood leaves its mark on the mineral matter filling the pith-cavity. Between the furrows thus produced we find the projecting ridges, corresponding to the medullary rays which had decayed. Ultimately the wood itself became reduced to a carbonaceous film, leaving the cast within visible.

On a well-preserved Calamitean cast, a little pro-

jection is almost constantly found on each ridge, immediately below the node.[1] Various explanations have been given of these projections, but a remarkable specimen in the Williamson Collection has settled the question. This specimen is a medullary cast of the base of a branch. It owes its interest to the fact that we not only find the little projecting bumps in their usual position, but that many of them are represented by regular spokes, radiating out for a long distance from the cast. Williamson found, in the specimens with internal structure preserved, that there was often a radial canal passing through the parenchyma of each principal medullary ray, near its upper end, which is sometimes dilated. These "infranodal canals," as he called them, extend through the entire thickness of the secondary wood. In other cases, where there is not a definite empty space, or canal, we still find that below the node the rays are dilated, their tissue in this part differing from that of the rest of the ray (see Fig. 8, *i.c.*, and Fig. 9, *c*). The dilated, infranodal portions of the rays extend far out into the wood, even when the rest of the ray is bridged over by intercalated tracheae.

Williamson's explanation was that these canals, whether natural or, as is more probable, left by decay, had, like the pith itself, become filled with mineral matter, giving rise in ordinary cases to elevations on the cast, which fitted into the hollow canals. In the remarkable specimen referred to, the canals had been filled throughout the whole thickness of the wood, and, when the wood itself perished, the mineral casts of the

[1] Clearly shown in Figs. 2 and 3, pp. 17 and 18. In Fig. 3 these prints are marked *i.c.* on the right.

canals were left behind intact.[1] In this exceptionally beautiful case, these radiating spokes correspond in size, shape, and position to the dilated infranodal rays, shown in so many of the specimens with structure. We know, from the evidence of the medullary casts with branches, that the prints in question occurred *below* the nodes (see Figs. 2 and 3): it follows that the dilated rays, or "infranodal canals," when present, were also below the node, and this fact is often of value in determining the top and bottom of a specimen in doubtful cases (cf. Figs. 8 and 9).

[1] This specimen is figured by Williamson in Part ix. of his memoirs "On the Organisation of the Fossil Plants of the Coal-measures," *Phil. Trans.* 1878, Part ii. Plate xxi. Fig. 31.

CHAPTER III

EQUISETALES—FRUCTIFICATIONS AND CLASSIFICATION

Calamostachys; Palaeostachya; Cingularia; Archaeocalamites; Macrostachya; Classification of Calamarieae; Mesozoic Equisetales.

1. *The Fructifications.*—We have now to consider the important subject of the fructifications of the Calamarieae. There are four main types of cone referred to this group, and known to us in some detail, though no doubt there are many more not so thoroughly investigated. First we will take the type of *Calamostachys*, representatives of which, with structure preserved, are common in the English Coal-measures. This genus is characterised by the fact that the cone does not merely bear whorls of peltate sporangiferous scales, as in *Equisetum*, but that the successive fertile whorls are separated from one another by intermediate and equidistant verticils of sterile bracts (see Figs. 17 and 21). The peltate scales by themselves look like those of an Equisetaceous fructification (see Figs. 18 and 20). It is better to use the word *sporangiophore* in this connection, rather than sporophyll, for, as we

shall see, the fossil forms considerably disturb current morphological ideas. Secondly, there is the *Palaeostachya* type, distinguished by the fact that the sporangiophores are not inserted midway between the whorls of sterile bracts, but immediately above each verticil of bracts, and, as it were, in its axil (see

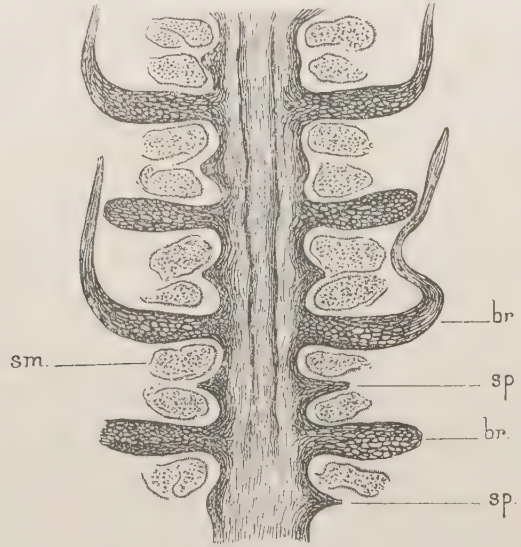

FIG. 17.—*Calamostachys Binneyana*. Radial section of part of cone, showing four whorls of bracts (*br*) with the sporangiophores (*sp*) between them, the peltate part not shown. *sm*, sporangia. × 8. Will. Coll. 1022. (G. T. G.)

Fig. 24, A, p. 61). The third type is one about which we do not know so much as we should like, because the remains are not preserved with structure, but only as impressions. This is the *Cingularia* type, which is just the reverse of that of *Palaeostachya*, for in *Cingularia* the sporangiophores are inserted immediately *below* the bracts, instead of immediately *above* them (see Figs. 28 and 29, pp. 68 and 69). Fourthly, we

have a type which is essentially the same as that of *Equisetum*, *e.g. Archaeocalamites*, for here the sporangiophores are present alone, without any bracts at all, or only at long intervals (Fig. 24, B). In other cases cones have been found which even more exactly resemble those of recent Equisetaceae.

2. *Calamostachys*.—I will now shortly describe the

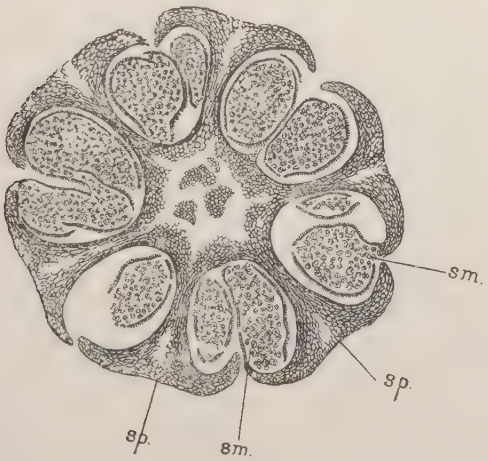

FIG. 18.—*Calamostachys Binneyana*. Transverse section of cone, passing through a whorl of six peltate sporangiophores, *sp*. *sm*. sporangia attached to the peltate laminae of the sporangiophores. × 16. Will. Coll. 1020. (G. T. G.)

British species of *Calamostachys*, the genus with alternating and equidistant whorls of bracts and sporangiophores. The affinities of the genus have been very much disputed in the past, but are now cleared up. We will first take the anatomy of the axis of the cone, as shown in the commonest British form, *Calamostachys Binneyana*. The axis is traversed by a central cylinder (see Fig. 17), with a distinct and persistent pith (see Fig. 19). Surrounding the pith are the vascular bundles,

of which there are usually six, sometimes eight; generally they are in pairs, the two at each corner being more or less fused. On the inner side of the wood of each bundle we find a more or less regular canal (*px* in Fig. 19). If we examine a radial section we see the spiral protoxylem-elements in the canals: we have thus essentially the same structure as in

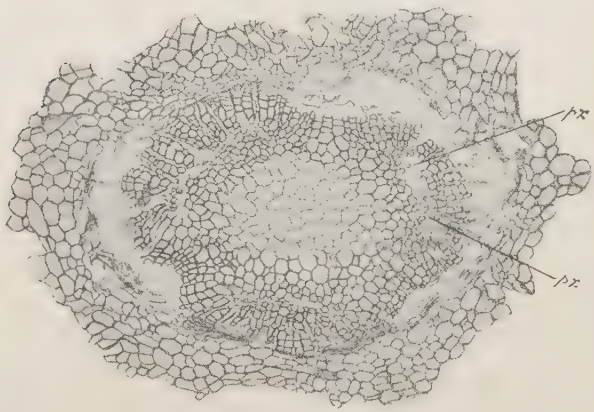

FIG. 19.—*Calamostachys Binneyana.* Transverse section of axis of cone, showing stele and part of cortex. Surrounding the pith there are six bundles, in groups of two, with secondary wood. *px*, protoxylem groups. × about 60. *Phil. Trans.* W. and S. Will. Coll. 1016.

Calamites, for the vascular bundles are collateral here also, as shown by specially favourable preparations, in which the phloëm can be recognised outside the wood; in *Calamostachys Binneyana*, however, there is a solid pith, and the bundles are comparatively few. A very important point is, that in most of these fructifications we find distinct indications of secondary wood in the axis (Fig. 19).

The bundles in *Calamostachys* do not alternate at

the nodes, but go straight down the axis. We see, however, that the anatomy, on the whole, is quite consistent with that of the Calamitean type of stem.

We will now pass on to the structure of the appendages, and will take the sterile bracts first. In our species (*C. Binneyana*) the bracts are coherent for a considerable distance from their insertion (see Fig. 21). In other species they are free, the whole way through. Through the coherent horizontal disc the vascular strands, springing from the node, pass out, entering the free tips of the bracts, which turn vertically upwards (Fig. 17). The structure of the bracts is much like that of the small vegetative Calamitean leaves, described above, but in the bracts, assimilating tissue appears to have been absent, and fibrous elements, especially in the apical portions, are strongly developed.

The whorls of peltate sporangiophores alternate with those of the sterile bracts, the number of the former in each whorl being often about half that of the latter. Thus in *Calamostachys Binneyana* there are commonly six sporangiophores and about a dozen bracts in their respective verticils (see Fig. 18), though in other cases there may be eight sporangiophores, while the number of bracts remains at about twelve. The sporangiophores have the same peltate form which is so familiar to us in *Equisetum*, but in *Calamostachys* each peltate scale bears four sporangia only, attached in a pendent position to the corners of the lamina (Figs. 18 and 20), which has a somewhat square form when seen in superficial view. A vascular bundle runs to the base of each sporangium. In tangential sections of the cone a group of four sporangia, diagonally

placed, surrounds the stalk of each peltate scale (see Fig. 21).

The sporangia are elongated sacs, stretching back from the lamina to the axis (Figs. 18 and 20). The sporangial wall, as preserved, is usually only one cell thick, and the lateral membranes of its cells are stiffened by projecting ridges (Fig. 22). When cut across, these

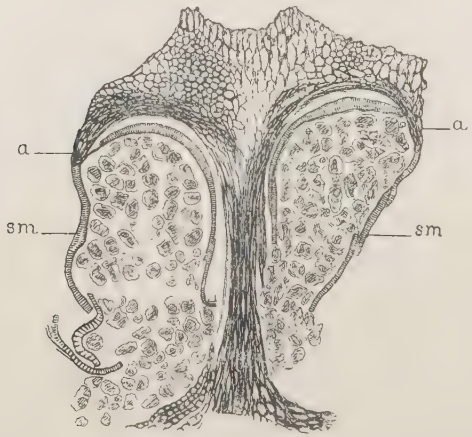

FIG. 20.—*Calamostachys Binneyana.* A single peltate sporangiophore, in longitudinal section. *sm*, sporangia, attached at *a* to the edges of the peltate lamina. They are full of spore-tetrads. × about 40. S. Coll. 174. (G. T. G.)

buttresses are not easily distinguished from the cell-walls.

In *Calamostachys Binneyana* the spores are very numerous in each sporangium, and, so far as has been ascertained, were all of one kind, the average diameter of the full-grown spores being about .09 mm. Curiously enough, we often find them united in groups of four, the tetrad being still enclosed within the membrane of its mother-cell (see Fig. 22, A, B, C). Hence we see that

the fourfold division, so general in spore mother-cells, already prevailed among these Palæozoic plants. In many cases the spores of the same tetrad are very unequally developed, some remaining quite small (Fig. 22, B and C); we may regard the latter as abortive spores, their suppression having allowed of the better nutrition of their surviving sister-cells. The mature spores show a triradiate marking on one side, probably

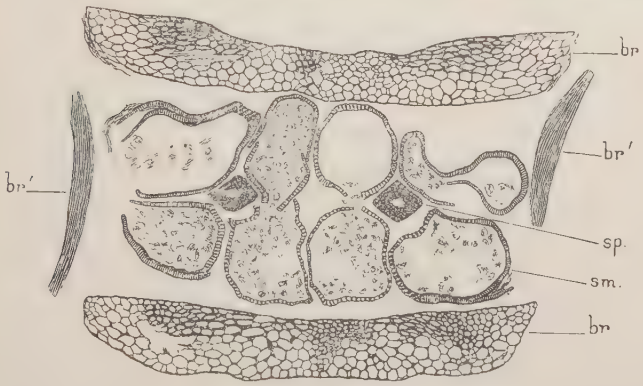

FIG. 21.—*Calamostachys Binneyana.* Part of tangential section of cone, showing portions of two whorls of bracts (*br*) with sporangiophores (*sp*) between. Around each of the latter the four sporangia (*sm*) are grouped. *br'*, free tips of other bracts. × about 25. S. Coll. 175. (G. T. G.)

indicating the lines of junction with the sister-cells (Fig. 22, D).

Numerous specimens of *C. Binneyana*, which is a fairly common fossil, have been examined, and no traces of more than one kind of spore have been found. Except for occasional abortion all the spores are uniform. There is thus a strong presumption that this species was homosporous. In another British species, however, *Calamostachys Casheana*, heterospory, as Williamson discovered, certainly occurred. In general organisation this cone is

practically identical with the homosporous species *C. Binneyana*, the differences between them being of a trivial kind. In some of the sporangia, however, numerous small spores are contained—slightly smaller than those

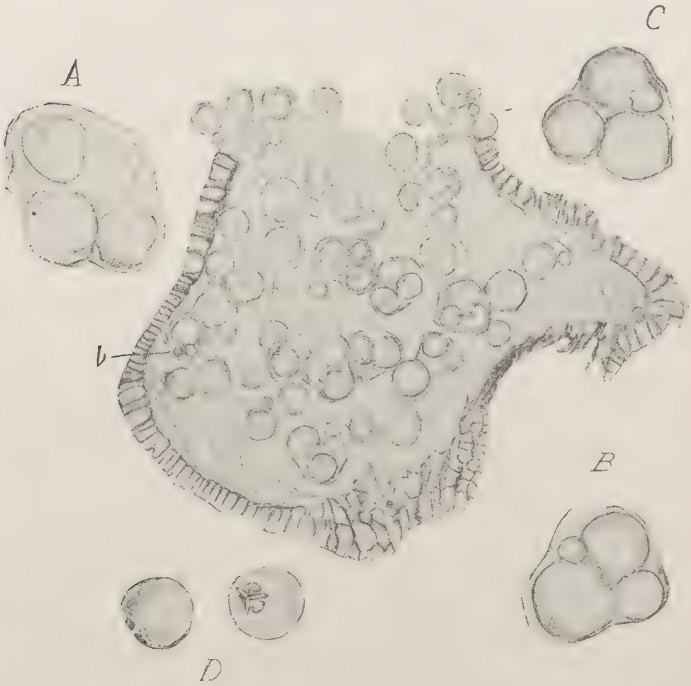

FIG. 22.—*Calamostachys Binneyana.* A single sporangium, containing spores in tetrads. Many of the spores are abortive (*b*). The structure of the sporangial wall is well shown. × 100. A. Tetrad with all four spores about equal. B, C. Tetrads, each with one abortive spore. D. Ripe spores showing the triradiate marks. A-D × 200. *Phil. Trans.*, W. and S. Will. Coll. 1011, etc.

of *C. Binneyana*, while other sporangia on the same cone, and sometimes on the same sporangiophore, contain a much smaller number of large spores, the diameter of which is just three times that of the former (see Fig. 23). Here, therefore, we have a perfectly clear case of a

heterosporous Calamarian cone, and some of the species from the Continent show the same phenomenon. The difference between microspores and megaspores, though well marked, is, however, less extreme than in the heterosporous Lycopods or Rhizocarps.

We saw, in the case of *C. Binneyana*, that some of the spores were abortive, and this is a point of some importance, because we know that a similar process of

FIG. 23.—*Calamostachys Casheana*. Tangential section, showing four sporangia grouped around their sporangiophore (*sp*). Three contain megaspores and one microspores. × 30. *Phil. Trans.* W. and S. Will. Coll. 1587.

abortion goes on in heterosporous, as well as in some homosporous Cryptogams, at the present day. It is an interesting fact that in the heterosporous *C. Casheana* we also find this abortion of some of the spores, but it is confined in this species to the megasporangia. It seems then that in this genus we are able to trace how heterospory originated. The facts suggest that in the first instance a certain number of spores became abortive, and so allowed of better nutrition for the remainder;

this process, going on more freely in some sporangia than in others, may ultimately have rendered possible the excessive development of those spores that survived, at the expense of the others, and may thus have led to the development of specialised megaspores.

In the heterosporous species, *Calamostachys Casheana*, the axis of the cone formed a zone of secondary wood, precisely as in the homosporous form, *C. Binneyana*, shown in Fig. 19. This fact is of considerable significance, in view of the excessive importance which palæobotanists have sometimes attached to secondary growth, as an indication of Phanerogamic affinities.

We have next to consider the relation of *Calamostachys* to *Calamites*. Neither of the British species described has as yet been found in connection with the stem or with vegetative organs of any kind. On the other hand, very similar Continental species have been found with such connection. In the *Calamostachys Ludwigi* of Carruthers,[1] for example, from the German Coal-measures, the spikes are borne upon a ribbed stem with whorled leaves, agreeing exactly with the smaller Calamitean twigs. In this species the structure of the cone is perfectly well known; it is that characteristic of the British forms of *Calamostachys*, except that in *C. Ludwigi* the bracts of the cone are free, instead of being coherent. This fossil thus affords certain evidence that fructifications of the *Calamostachys* type were borne on Calamitean stems,[2] a fact fully recognised by Mr. Carruthers, in his memoir of 1867, just cited.

[1] Carruthers, "On the Structure of the Fruit of *Calamites*," Seemann's *Journal of Botany*, vol. v. 1867. At that time the generic name *Volkmannia* was used for Calamarian strobili.

[2] See Weiss, *Steinkohlen-Calamarien*, ii. p. 163; Atlas, Plates

The evidence from comparative anatomy is also of considerable importance. The anatomy of the axis of the British forms of *Calamostachys*, which we have described fully above, although it agrees sufficiently well with that of *Calamites* to allow of the probability of relationship, is not exactly that of a Calamitean stem. It is very interesting to find that in some of the Continental species this difference does not exist. They combine the exactly typical anatomy of the Calamitean stem with the external morphology of a *Calamostachys*. This is the case, for example, in the fructification originally described by Renault under the name of *Bruckmannia Grand'Euryi*, which is, to all intents and purposes, a *Calamostachys*, and is placed by Count Solms-Laubach [1] in that genus.

In this case the anatomy of the axis is peculiarly well shown; there is a fistular pith, surrounded by a ring of eighteen collateral vascular bundles, and beyond that the cortex. Each bundle has a canal, perfectly defined, at the inner margin of its wood. In fact, the anatomy of the axis is that of a young stem of *Calamites*, so that the species *Calamostachys Grand'-Euryi* completely removes any anatomical difficulties we might find in referring *Calamostachys* to Calamitean stems. At the node each bundle gives off two strands

xxii.-xxiv., in *Abhandlungen zur geologischen Specialkarte von Preussen*, Band v. 1884. In the plates cited the structure of *C. Ludwigi* is magnificently illustrated.

[1] *Fossil Botany*, English edition, p. 329. M. Renault named this fructification *Arthropityostachys Grand'Euryi; Bassin houiller et permien d'Autun et d'Epinac, flore fossile*, Part ii. p. 135, Plate lxii., 1896. See also his *Cours de botanique fossile*, vol. ii. p. 136, Plates xxi. and xxii., 1882. The structure of this cone is preserved with extraordinary perfection.

to the bracts, which are here twice as numerous as the main bundles. According to Renault the strands supplying the sporangiophores also spring from the bract-node, pass up through a considerable part of the internode above, and then bend downwards and outwards to enter the sporangiophores. (Cf. Fig. 27 from *Palaeostachya*).

The morphology of the cone is in all respects that of a *Calamostachys*. There are the usual alternate whorls of bracts and sporangiophores, and the bracts in each whorl are twice as numerous as the sporangiophores. As in *C. Binneyana*, the bracts are connate in their lower portion, forming a continuous horizontal disc. The sporangiophores are of peltate form, and each bears four sporangia, exactly as in the species above described. Thirty-six bracts and eighteen sporangiophores were counted in their respective verticils.

I must add that some of the Continental species of *Calamostachys* (including *C. Grand'Euryi*) present a complication not found in the English species above described; this peculiarity consists in the presence of radiating vertical wings of tissue connecting each peltate scale with the whorl of bracts just above it. There was thus a membrane connecting the upper edges of the sporangiophores with the lower side of the bracts; in some cases a similar but less complete membrane also extended *downwards* from each sporangiophore. The sporangia thus lay in groups of four in the compartments formed by these radial plates of tissue. We have here one example among many of the complexity of the Palæozoic Cryptogams, as compared with those of the present day.

3. *Palaeostachya.*—We will now go on to the second main type of Calamarian fructification, that described by Weiss under the name of *Palaeostachya.*[1]

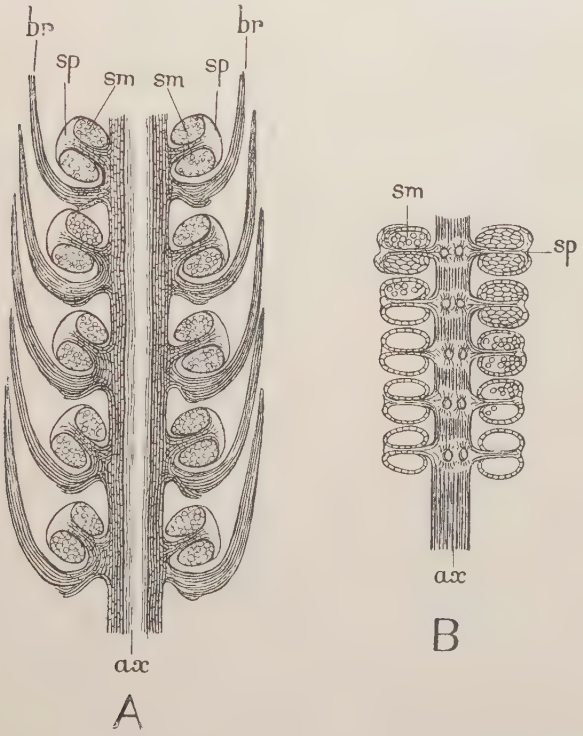

FIG. 24.—A. *Palaeostachya.* Radial section of cone, showing peltate sporangiophores (*sp*) inserted in axils of bracts (*br*). *sm*, sporangia; *ax*, axis of cone. Magnified. Diagrammatised after Renault. B. *Archaeocalamites radiatus.* Part of cone, showing axis (*ax*) bearing sporangiophores (*sp*) only. *sm*, sporangia. Magnified. After Renault.

Its peculiarity consists in the fact that the sporangiophores, instead of being inserted midway between the whorls of bracts, are placed in their axils. In

[1] *Steinkohlen-Calamarien*, i. p. 103, 1876.

Palaeostachya gracilis, described by Renault,[1] each whorl of bracts has about twenty members; the sporangiophores, about ten in each verticil, are inserted immediately above the bracts, in the angle between the latter and the axis. In the diagrammatic Figure, 24, A, the position of the sporangiophores is well shown. In Fig. 25 another species, *Palaeostachya pedunculata*, is represented on a small scale, as in the actual specimen. In this case a large number of cones are seen attached to a Calamarian branch.

FIG. 25. — *Palaeostachya pedunculata.* Specimen from the coal-shales, showing a fertile shoot bearing about a dozen cones and a few leaves. *k*, stem. About $\frac{2}{3}$ of nat. size. After Williamson, *Phil. Trans.* Will. Coll. 1060.

While the position of the sporangiophores in *Palaeostachya* is thus strikingly different from that in *Calamostachys*, their structure is almost identical. Each sporangiophore, as in that genus, is peltate, bearing four sporangia on its lower surface. The spores are of the same type as in the homosporous *Calamostachys*. The occurrence of

[1] This author uses the generic name *Volkmannia*, and refers these fructifications to the vegetative shoots known as *Asterophyllites*; see below, p. 70; Renault, *Cours de bot. foss.* vol. ii. p. 114, Plates xviii. and xix.; *Flore fossile d'Autun et d'Epinac*, p. 74, Plates xxix. and xxx.

heterospory is, however, proved in the case of another species perhaps referable to *Palaeostachya*.[1]

In *Palaeostachya gracilis*, according to Renault's observations, the number of sporangiophores in the whorl is about half that of the bracts, while the number of vascular bundles in the axis is equal to that of the sporangiophores in a whorl. In its anatomy, the axis closely resembles a young Calamitean stem.

A fructification belonging to the type of *Palaeostachya* was described by Dr. Williamson for the first time in 1869,[2] and subsequently much more fully in 1887.[3] This strobilus he called the "true fructification of *Calamites*," and, for many years, he refused to admit any other fructification as properly belonging to *Calamites*, the reason being that in this "true fructification" of his, and, as he thought, in no other, the Calamitean anatomy was manifest in all its essential points. In cases where we have both the peduncle and the axis, the former has in all respects Calamitean structure, including a secondary zone of wood, which dies out as the axis itself is approached. This form was called by Dr. Williamson in his last memoirs[4] *Calamites pedunculatus*. It was distasteful to him to give any other generic name than *Calamites* to a fructification which he felt so sure belonged to that genus. It is, however, more convenient to retain special

[1] Renault, *Flore fossile d'Autun et d'Epinac*, Part ii. p. 77, Plate xxix. Figs. 6 and 7.

[2] "On a New Form of Calamitean Strobilus," *Mem. Lit. and Phil. Soc. of Manchester*, 1869.

[3] "Organisation of Fossil Plants of Coal-measures," Part xiv., *Phil. Trans.* 1888, B.

[4] See Williamson and Scott, "Further Observations, etc.," Part i., *Phil. Trans.* vol. 185, B, 1894, p. 916.

generic names for the cones, as it is so rarely possible to refer them to particular forms of stem; while, as we have already seen, some forms of *Calamostachys* have as good a claim as *Palaeostachya* to be referred to the genus *Calamites*. Williamson's specimen has therefore been re-named *Palaeostachya vera* by Mr. Seward, the specific name serving to recall Williamson's original description of the fructification.[1]

The Calamitean anatomy is shown with great perfection both in the peduncle and in the axis of the strobilus; in the canals accompanying the vascular bundles, the disorganised spiral tracheae are found, just as in the vegetative stem. In this form the number of sporangiophores is from sixteen to twenty in each whorl, the bracts, which were connate at their base, being, according to recent observations by Mr. George Hickling,[2] about equal in number, as are also the vascular bundles in the axis. Fig. 26 represents a transverse section of the cone. The vascular bundles are here approximated in pairs, the pairs alternating, in the nodal region, with so-called canals, which represent parenchymatous areas in the sclerotic disc which strengthened the node. The peltate part of the sporangiophores is imperfectly preserved in the English specimens, but the sporangia are well shown, and are, as usual, four in number on each sporangiophore. The structure of the sporangial wall is identical with that of *Calamostachys*. The spores, so far as the existing specimens show, were all

[1] The specific designation *pedunculata* was inadmissible, as it had been previously given to a different species of *Palaeostachya*, namely that shown in our Fig. 25.

[2] The anatomy of *Palaeostachya vera*, *Annals of Botany*, vol. xxi. July 1907.

of one kind, and of similar dimensions to those of *Calamostachys Binneyana*.

The apparently axillary position of the sporangiophores in *Palaeostachya* evidently suggests caution in

FIG. 26.—*Palaeostachya vera*. Transverse section of cone. Surrounding the fistular pith is the ring of bundles (*vb*) grouped in pairs. Outside them is the cortex and disc (*c*). *sp*, pedicels of the sporangiophores, some shown attached to the axis, others between the sporangia (*sm*), which are grouped in fours around the sporangiophores; *sp'*, remains of peltate lamina of a sporangiophore; *br*, bracts. × about 7. S. Coll. 474. (G. T. G.)

accepting the current view that these organs in Equisetineae are simply leaves. Mr. Hickling's observations have cleared up, for the first time, the course of the vascular strands which supply the sporangiophores. He finds that they start from the same node as the

bundles which run to the subtending bracts, and immediately above them. The sporangiophore bundle, however, passes vertically upwards, parallel to the corresponding main bundle of the axis, until it has ascended through almost exactly half the internode.

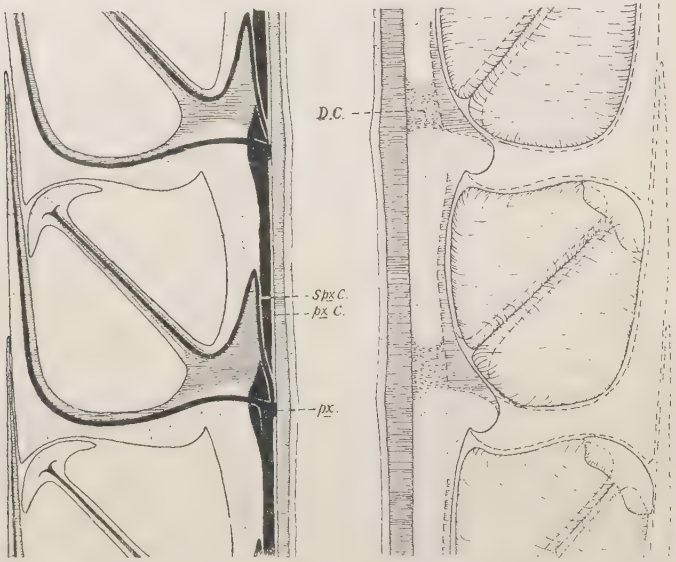

FIG. 27.—*Palaeostachya vera.* Diagrammatic longitudinal section of cone. Vascular tissue, *black*; soft parenchyma, *dotted*; sclerised, *lined*. *Left* side passes through bundle; *right*, between bundles. Sporangia omitted on left side; inserted on right in surface-view. *D.C.*, disc canal; *px.C.*, protoxylem canal of main bundle; *Spx.C.*, protoxylem canal of sporangiophore trace; *px.*, persistent protoxylem at the node. Note the sharply reflexed course of the bundles supplying the sporangiophores. From Hickling.

It is then sharply reflexed, descends rapidly to the upper limit of the nodal disc, and sweeps horizontally across the upper part of this to the base of the sporangiophore, which it enters[1] (Fig. 27). Thus in *Palaeostachya*, as in *Calamostachys*, the evidence of the

[1] Hickling, *l.c.* p. 375.

vascular supply indicates that the sporangiophores may be regarded as the ventral appendages of the bracts subtending them. On account of the anomalous course of the sporangiophore bundles, Mr. Hickling regards *Palaeostachya* as derived from the *Calamostachys* type.

4. *Cingularia.*—We now come to the third type of the Calamarian fructifications which I shortly described above, namely that of *Cingularia*. Our knowledge of *Cingularia*, which is chiefly due to the researches of the German palæobotanist Weiss,[1] is less satisfactory than in the cases already considered. So far we have been dealing with fructifications with their internal structure preserved. *Cingularia* is not one of these; it is only known from carbonaceous impressions, and not from petrified specimens, and hence only its external characters are open to investigation. Under these circumstances we cannot feel the same certainty in the interpretation of the facts as in specimens with the whole structure preserved. We may, however, accept Weiss's description as being probably the correct one. The plant itself had the usual Calamarian habit, with a jointed stem and whorled leaves. It appears that the successive whorls were superposed, not alternating as in most Calamarieae. The fructifications were long, very lax cones, with the whorled appendages rather remote from each other (see Fig. 28).

The conclusion at which Weiss arrived is that each whorl was a double one, and that it consisted of a verticil of coherent bracts running out into sharp teeth at the edges, and of another coherent verticil immediately

[1] *Steinkohlen-Calamarien*, i. p. 99, Plates vi.-ix. 1876.

below the first, consisting of the sporangiophores (see Fig. 29). Thus the relative position of bracts and sporangiophores is just the reverse of that in *Palaeostachya*. According to Fischer's observations the bracts and sporangiophores were not free whorls, but were partly united to each other, an important point of

FIG. 28.—*Cingularia typica*. Part of branch, bearing whorled leaves and a lax cone, with whorled bracts. Nat. size. After Weiss.

analogy with the Sphenophyllales. (See next chapter, p. 99).[1] The strap-shaped sporangiophores separate from one another as they approach the exterior, and further to the outside each divides into two lobes, as shown in Fig. 29. Looking at the under surface of a fertile whorl, we notice on each of the flattened sporangiophores four prints, which are known to have

[1] See Ed. Fischer, "Einige Bemerkungen über die Calamarieen-gattung *Cingularia*," *Mitth. d. Naturf. Gesellsch. in Bern*, 1893.

been the points of attachment of the sporangia, as the latter are occasionally found *in situ*. Each of the sporangiophores thus bore four sporangia on its lower surface (Fig. 29). The sporangia were of approximately spherical form, and remarkably large, averaging 5 mm. in diameter, which is five times the size of the sporangia of *Calamostachys Binneyana*. The number of bracts in

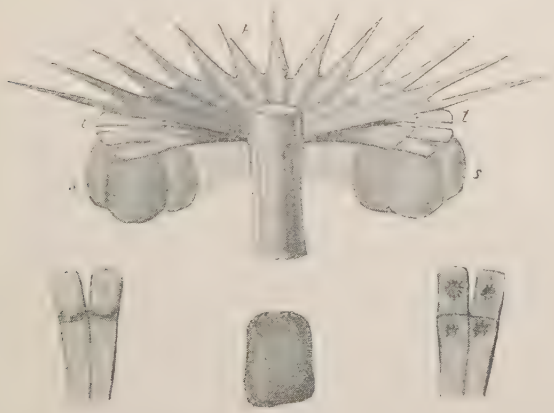

FIG. 29.—*Cingularia typica*. Enlarged diagram of a verticil of the cone, showing the connate bracts (*b*) above, and the strap-shaped sporangiophores (*l*) below, bearing the sporangia (*s*). The small figures show two sporangiophores, that on the left seen from above, and that on the right from below. In the middle a sporangium. After Weiss.

a whorl seems to have been equal to that of the sporangiophores. The great peculiarity of *Cingularia* consists in the fact that the sporangiophores lie immediately below the sterile bracts of each whorl, instead of immediately above them, as in the last type. This is different from anything we are accustomed to find among other Pteridophyta. In the absence of better evidence than we at present possess, it is impossible to draw any decisive conclusions as to the

morphology or affinities of *Cingularia*. We cannot be absolutely certain of the accuracy of our interpretations, and still less can we be certain whether we have to do with a Calamarian or a Sphenophyllaceous plant. These questions can only be cleared up if specimens with the structure preserved should be discovered.

5. *Archaeocalamites*.—A fourth type of Calamarian fructification remains to be noticed. This is a simple one to describe, because it has much in common with that of the only surviving genus of Equisetales, the recent *Equisetum*. The remarkable genus *Archaeocalamites*, characteristic of the oldest Carboniferous strata and of the Upper Devonian, appears, according to M. Renault's observations, to have borne the fructification of which a fragment is represented in Fig. 24, B. The cones occur associated with the stems and dichotomous leaves of that genus, though the evidence from actual continuity is wanting. The cone bears whorls of sporangiophores, from eight to ten in each whorl; they have the usual peltate form, with the expanded portion little developed, and each appears to have borne four sporangia. Sterile bracts are not shown, but it is quite probable that they may have occurred in scattered whorls, at long intervals, as was clearly the case in the genus *Pothocites*, associated with *Archaeocalamites* in the Lower Carboniferous of Scotland. *Pothocites* consists of large cylindrical strobili, constricted at intervals, the constrictions no doubt marking the position of the sterile whorls.[1] The

[1] See Kidston, "Affinities of the Genus *Pothocites*," *Trans. Bot. Soc. Edinburgh*, 1883.

fructifications of *Archaeocalamites* are not yet known in the petrified condition.

Archaeocalamites is a very ancient type of Calamarian tree, characterised by the non-alternation in successive internodes of the furrows on the casts corresponding to the vascular bundles, and also by the

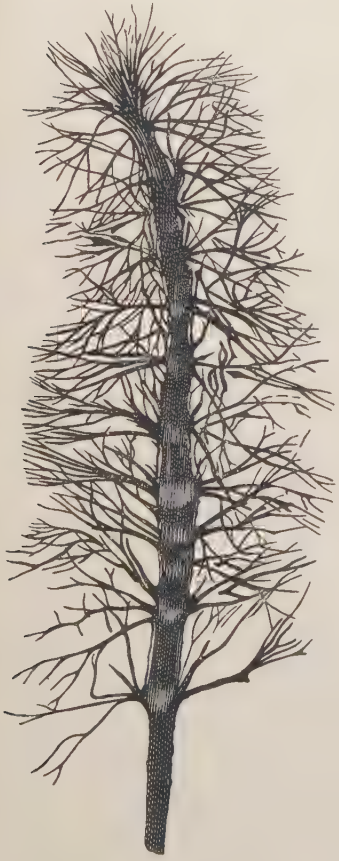

Fig. 30.—*Archaeocalamites radiatus.* Branch bearing whorled leaves, which are dichotomously subdivided. Half nat. size. After Stur.

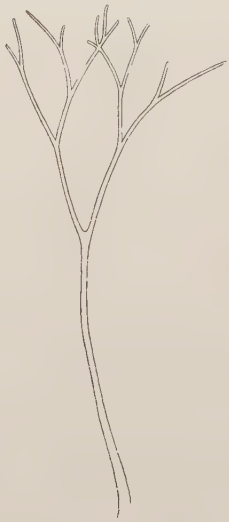

Fig. 31.—Single leaf of the same. Half nat. size. After Stur.

remarkable foliage, for the leaves were forked, instead of being simple.[1] Fig. 30, from a work by the Austrian

[1] The anatomy of the stem of some species of *Archaeocalamites* has been worked out by M. Renault and Count Solms-Laubach, and is described

palæontologist, Stur, gives a good idea of the habit of a leafy branch, and in Fig. 31 a single, repeatedly forked leaf is shown. M. Grand'Eury has discovered fructifications resembling the cones of living Equisetaceae, from the French Coal-measures, and Mr. Kidston has described, under the name of *Equisetum Hemingwayi*, a large cone, which presents the external characters of a fructification of the recent genus. There is altogether a considerable amount of evidence to show that fructifications of the *Equisetum* type already existed in the Coal-period, but unfortunately none of the specimens in question have their internal structure preserved. The Permian plant known as *Phyllotheca deliquescens*, has a fructification presenting some analogies with *Pothocites*, the long fertile spikes being interrupted at intervals by whorls of sterile leaves. A similar condition occurs as an abnormality in recent species of *Equisetum*.

6. *Macrostachya.*—In addition to these well-characterised types, we have various fructifications which have been referred to Calamarieae, but as to which our information is contradictory and scanty. Among these it is only necessary to mention the genus called *Macrostachya*, the cones of which are of great size, attaining 8 inches in length by an inch or more in diameter (see Fig. 32). They were often borne in whorls, on stout stems with typical Calamitean structure,

as exactly that of an ordinary Calamite, of the kind in which the medullary rays become bridged over by interfascicular wood. The roots were of the "*Astromyelon*" type. See Renault, *Flore fossile d'Autun et d'Epinac*, Part ii. p. 80, Plates xlii. and xliii.; and Solms-Laubach, *Botanische Zeitung*, 1897, p. 219. It is possible, however, that the Lower Carboniferous Calamarian stem, with centripetal wood, described on p. 36, may have belonged to an *Archaeocalamites*.

and these cones are among the most striking fossils of the Coal-period. There is great doubt as to the internal structure of the cones. M. Renault examined the carbonised cones of a *Macrostachya*, found in connection with the stem, which was of the *Calamitina* type (see below, p. 74), and showed the usual Calamitean structure. The fructification proved to be heterosporous, the microsporangia and megasporangia occurring on the same strobilus, as is the case in *Calamostachys Casheana*.[1]

FIG. 32.—*Macrostachya infundibuliformis*. Cone borne laterally on a branch. Half nat. size. After Weiss.

7. *Classification.*—Before leaving the Calamarieae I must say a few words as to their classification. This is a most difficult, and indeed in the present state of our knowledge, insoluble question, because we only have the plants as preserved in the form of fragments. Consequently, we shall not be surprised to find that the classification of Calamarieae has been based on totally different principles, according to the parts of the plants selected. For example, Weiss classified Calamarieae by means of the characters presented by their medullary casts, and more especially according to the form and distribution of the scars marking the position of the branches. For the purposes of geologists his is

[1] *Notice sur les Calamariées*, Part iii., Autun, 1898.

a useful arrangement.[1] Again, we may classify these plants with reference to the structure of their wood. We have ourselves distinguished the simple structure of *Arthropitys* or *Calamites* proper from the more complex organisation of *Calamodendron*, between which the *Arthrodendron* form is intermediate. Then again it might be possible to arrange them according to their foliage, and as we shall see, considerable use has actually been made of characters drawn from the leaves. For example, the simple leaves of most Calamarieae contrast sharply with the dichotomous leaves of the *Archaeocalamites* type. A far better plan would be to classify the specimens according to the fructification, the character on which we should chiefly rely in the case of recent plants. But we have not yet any scheme which combines all these characters into a natural classification of the plants themselves, and, from the nature of the material, such a scheme is chimerical, though a slow approach towards it may be made, as new evidence accumulates.

I may give a short summary of an attempt made in this direction by the French palæobotanist Grand'Eury, who has the advantage of knowing more about the Calamarieae and other fossil specimens, as they occur underground, than any other authority. His position as a mining engineer has given him unrivalled oppor-

[1] Weiss's subgenera may be shortly characterised as follows:—*Stylocalamites*: branches few, and irregularly scattered (see Figs. 2 and 3). *Calamitina*: internodes usually short; branches in whorls, limited to certain nodes, often surmounting internodes shorter than the rest. *Eucalamites*: branches on every node, in some cases one, in others many, on each. *Archaeocalamites*: ribs continuous, not alternating as in the three former; branches limited to certain regions of the stem, where they are present on every node. See *Steinkohlen-Calamarien*, Part ii. 1884.

tunities of observing the fossils *in situ*. Grand'Eury [1] distinguishes three great groups, represented respectively by *Annularia*, *Calamites* proper, and *Calamodendron*. The first group, *Annularia* (Fig. 33), is characterised by whorled leaves, usually more or less lanceolate in shape, attached to a stem of Calamitean structure, which is said to have attained only a small diameter, not exceeding 2 or 3 inches in the forms described. The structure of the finer branches is very delicate, and the plants have been supposed to be herbaceous aquatics. There is, however, very little evidence for this, and there is reason to believe that some at least of the *Annulariae*, as, for example, *A. stellata*, were simply the branches of large Calamites. It has lately been shown that in this latter form the leaves were united at the base, to form a regular sheath, as in the recent *Equiseta* [2] (cp. Fig. 12, p. 38). The fructifications of the *Annulariae* are called by Grand'Eury and Renault *Bruckmannia* ;

FIG. 33.—*Annularia brevifolia*. Twigs, bearing whorled leaves. Nat. size. After Stur.

[1] *Bassin houiller du Gard*, St. Etienne, 1890, p. 200.

[2] See Potonié, "Aeusserer Bau der Blätter von *Annularia stellata*," etc., *Verhandl. bot. Ver. d. Prov. Brandenburg*, Bd. xxxiv.

they are identical in structure with our *Calamostachys*, and some of them are known to have been heterosporous.

Secondly, according to Grand'Eury, we have the great division of *Arthropitys*, or *Calamites* proper, of which *Asterophyllites* represents the foliage, or rather the leaf-bearing branches. There appears to be good evidence for the connection between them. The wood, where preserved, is of the simple type of *Calamites* or *Arthropitys*, described in detail in the last chapter. The characteristic arrangement of the spikes is in panicles borne on branches with the foliage of *Asterophyllites* (cf. Fig. 25). The terminal leaf-bearing branches were distichously arranged, with crowded whorls of narrow acicular leaves, which here also were united when young into a sheath (see Fig. 34). Associated with the Calamitean stem, and in connection with the Asterophyllitic foliage, is found *Palaeostachya gracilis*, which was one of the forms of fructification belonging to this type, a fact which agrees with Williamson's results, but cones of the *Calamostachys* form also belonged to this group. In fact, the whole position is rather paradoxical, for to the stem known specifically as *Calamites cannaeformis* (according to the characters of the medullary cast) Grand'Eury attributes fructifications of two different genera! This shows that the so-called species among fossils must not be understood in the same sense as species of living plants. Grand'Eury himself points out that these so-called species are rather of generic value. It is no doubt impossible to recognise strictly specific differences from the medullary casts, and it is quite likely that stems with casts indis-

tinguishable from one another may even have borne fructifications as different as those of *Palaeostachya* and

FIG. 34.—*Asterophyllites densifolius.* Branch bearing distichously arranged twigs; both branch and twigs with verticillate leaves. Somewhat restored. After Grand'Eury.

Calamostachys. The branches were arranged in whorls limited to certain definite nodes (*Calamitina* of Weiss's

nomenclature), and the aërial stems sprang from subterranean rhizomes.

I should mention that *Macrostachya* fructifications are found in association with the same type of stem. In France this group seems to have been found chiefly in the Middle Coal-measures, and not to extend into their upper beds.

Grand'Eury's third type is *Calamodendron*, found only in the upper beds of the Coal-measures. This horizon appears to be represented in England by the Somersetshire coal-field, but petrified specimens have not been recorded from it, and at present stems of the *Calamodendron* type of structure have not been obtained from our coal-fields. Grand'Eury associates with the *Calamodendron* wood (described above) some small cones, to which he gives the name of *Calamostachys* (but not, as used by us, in the sense of Schimper), and certain leafy branches quite distinct in character from *Asterophyllites*; these he calls *Calamocladus*. *Calamocladus* is characterised by the whorls of leaves being separated by long internodes, and not crowded together as in *Asterophyllites*, and also by the fact that the upper branches were not arranged distichously, but radiated out on all sides. The leaves are said to have had several nerves, instead of a single median one, as in the former types. Grand'Eury brings forward good evidence that certain fructifications, usually of small dimensions, really belonged to the branches named *Calamocladus*. Some of these fructifications are described as having essentially the structure of the cones of recent *Equiseta*, bearing peltate scales only, without sterile bracts; the preservation, however, does

not seem to be good enough to settle the point for certain.

It appears that the stems with the structure of *Calamodendron* had much longer internodes than those of the *Arthropitys* type, and that the branches were scattered irregularly, and not limited to certain definite nodes as in the *Arthropitys* group. These and other differences are said to render the casts of *Calamodendron* recognisable ; they correspond to the *Stylocalamites* of Weiss's system. In *Calamodendron*, as in the former group, the upright stems sprang from subterranean or aquatic rhizomes. Grand'Eury believes that the development of the secondary wood, in Calamarian stems of the same type, increases as we ascend from the lower to the higher horizons of the Coal-measures.

In addition to the three groups just enumerated, we have the ancient genus *Bornia* or *Archaeocalamites*, with its forked leaves and fructifications of a somewhat Equisetiform character. There is another genus which Grand'Eury has distinguished under the name of *Autophyllites*; its fructifications are much like those attributed to *Bornia*, and it had large dichotomous leaves. The plant is of Upper Coal-measure age.

It is important to point out how nearly some of the Calamarieae of the Carboniferous period approached our living *Equisetum*. In some, as we have seen, the fructification was of a very similar type, and there is no longer any doubt that many members of the family had leaves coherent at the base, so as to form a regular sheath (see Fig. 12). It is probable, as already mentioned, that the sheath may often have become split, as the stem within grew in thickness, and that

this may account in certain cases for the apparently distinct leaves.

So far, I have treated the Calamarieae generally as being Cryptogamic plants with manifest Equisetaceous affinities, and I do not think, so far as that goes, that much difference of opinion now remains, though for many years their position was warmly disputed. I mentioned in the last chapter the views of Brongniart. His distinguished disciple, the late M. Renault, took the same side in the controversy, but, as time went on, considerably modified the original Brongniartian view. Brongniart would not have allowed that all the plants now grouped as Calamarieae were nearly allied to one another. He separated them sharply, at least in his later works, into two wholly different families, the one Cryptogamic, the other Phanerogamic.[1] M. Renault, on the other hand, recognised the family of Calamarieae, as including all fossil plants, *whether Cryptogamic or Phanerogamic*, which possess a "Calamitoid" stem.[2] Within this main group, however, he separated the Equisetineae (with Cryptogamic, homosporous or heterosporous cones) from the Calamodendreae; the latter he still inclined to regard as Gymnospermous Seed-plants. In his latest works he gave up the distinction based on the presence or absence of secondary wood, and recognised the existence of Cryptogamic Calamarieae with cambium, as in the case of the *Calamites* which bore *Macrostachya* as its fructification. Thus, in the end, there came to be substantial agreement between the great French palæobotanist

[1] *Tableau des genres de végétaux fossiles*, p. 49, 1849.
[2] *Flore fossile d'Autun et d'Epinac*, Part ii. 1896, p. 60.

and the English school, of which Williamson was the leader.

If M. Renault's view that a certain part of the Calamaricae bore seeds were tenable, we should have the remarkable case of a transition from Cryptogamic to Phanerogamic plants within the limits of a single family. For this conclusion, though not without analogy,[1] there is, as yet, no satisfactory evidence in this case.

M. Renault was led, by his belief in the existence of Phanerogamic Calamarieae, to regard some of the fructifications of the *Calamostachys* type as male cones, others as Cryptogamic strobili, a distinction which the identity of structure renders improbable, in the absence of more positive evidence. He also attributed certain highly developed seeds (*e.g. Gnetopsis* and *Stephanospermum*) to the Calamarieae, but this was never more than a conjecture, and on present evidence it appears that the affinities of the seeds in question lay in a totally different direction, *i.e.* with the Pteridospermeae (see Chapter X.). A specimen, named by M. Renault *Arthropityostachys Williamsonis*,[2] was interpreted by him, though with some doubt, as a Calamarian cone bearing at the same time both seeds of the *Gnetopsis* type and pollen-sacs, but this interpretation has not stood the test of further investigation.[3]

There is, in fact, no evidence, in the present state of our knowledge, that the Calamarieae were anything more than a varied and highly organised family of

[1] See below, Chapter VI. p. 193.

[2] *Flore fossile d'Autun et d'Epinac*, Part ii. p. 137, Plate lxiii.

[3] Cf. Zeiller, "Revue des travaux de paléontologie végétale," 1893-1896, in *Revue générale de botanique*, 1897, p. 371.

Vascular Cryptogams, closely allied to the recent Horsetails. But, although none but Cryptogamic Calamarieae are known to us, the question remains whether they show marked affinities to any of the groups of Seed-bearing Plants, or are likely to have lain on or near any of the lines of Phanerogamic descent.

If there were any such affinity, it would appear to lie in the direction of Coniferae, or possibly, as M. Renault suggested, of Gnetaceae. The anatomy of the stem certainly approaches that of the former family, while the usually simple form and structure of the leaves may be regarded as pointing the same way. Even the fructifications are not without analogy in the two groups. The relative position of the sporangiophore and bract in *Palaeostachya* has been compared with that of the ovuliferous and carpellary scale in Abietineae. I was at one time disposed to attach some weight to these various considerations, as indicative of affinity. It is more probable, however, that these points of resemblance between Calamarians and Conifers are nothing more than analogies—interesting examples of parallel development, but not marks of relationship. There is an entire absence of transitional forms between Equisetineae and either Coniferae or Gnetaceae, whereas, as we shall see later on, there is strong evidence for the derivation of the Gymnosperms generally (or at least of the Cycads and Conifers) from a different Cryptogamic stock, namely that of the Ferns.

8. *Mesozoic Equisetales.*—The Calamarieae hitherto considered are strictly Palæozoic plants; the last

survivors of the Calamites appear to have died out in the Permian at the close of the Primary period. The Equisetineae, however, were well represented during the Secondary epoch,[1] by forms in some respects intermediate between the Palæozoic Calamites and the recent Horsetails. In the Trias very large Horsetails are found, the stem of one of them, *Equisetites arenaceus*, even attaining a diameter of 20 cm. (8 inches). All parts of this plant—rhizome, aërial stem, leaf-sheaths, and cones—are preserved, and though all the organs are not in connection, there seems no reason to doubt that they really belonged to the same species. In all respects there is a close agreement with our recent Horsetails, but the Triassic plant was on an immensely greater scale; it had, for example, as many as 120 leaves in a whorl. It is probable that these great stems, like those of the still larger Palæozoic forms, possessed secondary tissues, but at present this is only a conjecture. In the Rhætic and Liassic *Equisetites* of Sweden M. Halle finds that the internodal bundles are three to four times as numerous as the leaf-teeth of a whorl; the bundles must therefore have traversed at least three internodes. In *Neocalamites*, a genus separated by M. Halle from *Schizoneura* (see below), the bundles passed through two internodes, apparently branching in some cases. These facts offer interesting analogies with the Palæozoic Calamites (see above, p. 26). Numerous Mesozoic species are known; on the whole their dimensions diminish as the later horizons are approached. Some of the fossil forms, as,

[1] For a fuller account of the Mesozoic Equisetales, see Seward's *Fossil Plants*, vol. i.

for example, *Equisetites Burchardti* from the Wealden, had tubers just like those of some recent species.

The genus *Phyllotheca*, very similar to *Annularia*, but with the leaves more united, appears to represent a Palæozoic type which extended into the Mesozoic period as far as the Lower Jurassic. *Schizoneura*, a characteristic Triassic genus, is remarkable for the splitting of the leaf-sheath into leaf-like segments of variable width. The Secondary Equisetales appear to offer a promising field for research. Professor Nathorst kindly informs me that M. Halle, who is investigating the Stockholm collections of Rhætic and Liassic Equisetaceae from Scania in Sweden, has succeeded in finding the sporangia on the lower surface of the peltate sporangiferous scales; this is the first time they have been observed in Mesozoic specimens. The sporangiophores, which appear to have been of an almost ligneous texture, have on their lower surface the prints of about twenty-four sporangia — a larger number than in the recent genus. The sporangia and spores closely resemble those of the recent *Equisetum*; the elaters, however, are not preserved. An interesting point is that the spores show a triradiate marking almost identical with that on the spores of *Calamostachys Binneyana* (cf. Fig. 22, D).[1]

From the rapid sketch of the fossil Equisetales which has now been given, it is evident how greatly our whole idea of the family is widened by the study of the extinct forms. It is from these alone that we

[1] At present M. Halle has only published a preliminary notice, in Swedish, of his interesting discoveries.

can form any conception of the variety of which this type of organisation is capable, and of the high differentiation to which it once attained. In fact, it is no exaggeration to say that, as regards this important Cryptogamic stock, the study of the fossil forms far outweighs in scientific interest that of the few humble species which have survived to our own day.

CHAPTER IV

SPHENOPHYLLALES

Sphenophylleae ; Cheirostrobeae ; Pseudoborniales

So far, we have been endeavouring to extend our knowledge of a class already familiar to us, by the study of its extinct representatives. We now go on to fill in a gap in the natural system in a different way, by the description of a group which appears so remote from any recent plants, that it is only quite within the last few years that its probable affinity with an isolated existing family (the Psilotaceae) has been detected. The class in question—that of the Sphenophyllales—was not, so far as our present knowledge shows, an extensive one, but it is of great phylogenetic interest.

I. Sphenophylleae

1. *Sphenophyllum—Vegetative Organs.*—The external aspect of the various species of *Sphenophyllum* has long been familiar to palæobotanists ; the specimens, when preserved in the form of impressions, are often among the prettiest of the Carboniferous remains. The genus, which is nearly co-extensive with the family

Sphenophylleae, is characteristic of the Carboniferous formation, and occurs throughout its whole extent, appearing also in the Permian immediately above it, but scarcely reaching the Triassic. The slender stems of *Sphenophyllum* were ribbed; the ribs did not alternate in successive internodes, but ran straight on through the nodes; in like manner, the leaves of successive whorls were not alternate, but superposed, a point of great importance among the distinctive characters of *Sphenophyllum*. In the typical species, on which the genus was founded, the leaves, usually six in a whorl, were wedge-shaped, with an entire or toothed margin (Fig. 35). It was soon found, however, that the wedge-shaped form of leaf was not universally present. In very many cases the leaves were dichotomously divided into narrow lobes, and in some we find a whorl of perfectly simple narrow leaves, which may be regarded as corresponding to the segments of a smaller

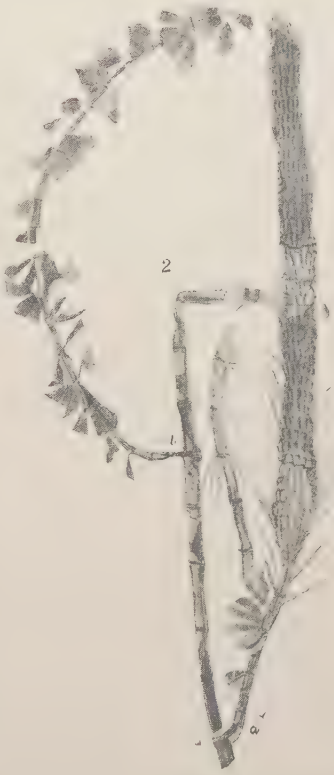

FIG. 35. — *Sphenophyllum*, sp. Branched stem, bearing linear and cuneate whorled leaves on different parts. The branch *a* terminates in a long and slender cone. Half nat. size. After Stur.

number of deeply-cut palmate leaves. In some members of the genus, both forms of leaf, the simple and the compound, are found on the same stem (see Fig. 35); and as, in certain cases, the finely-cut leaves are found below, and the broader wedge-shaped leaves above, a comparison has been suggested with the dimorphic foliage of many aquatic *Ranunculi*, and other water-plants of the present day. It is a familiar fact that in the Water Crowfoot, for example, the lower submerged leaves are finely divided into capillary segments, while the upper floating leaves are entire or but slightly lobed. Hence it was inferred that *Sphenophyllum* itself was an aquatic genus. But this comparison will not really hold good, for in *S. cuneifolium*, for example, the upper cone-bearing branches show the finely-cut foliage, while the leaves of the main stem are often cuneate.

Apart from this difference in the form of the foliage, there is considerable uniformity in the external characters of *Sphenophyllum*.[1] The stem was branched, the lateral branches springing from the nodes; their exact relation to the leaves has not yet been cleared up. The fructification consisted of fairly large cones (Fig. 35), which from their external appearance might in some cases very well be taken for those of the Calamarieae. We shall see, however, that their organisation was different.

[1] In *S. speciosum*, sometimes separated under the generic name *Trizygia*, derived from the Gondwana formation (probably Permo-Carboniferous) of India, the six leaves of each whorl are grouped in three pairs, one pair being constantly smaller than the other two. The leaves are accurately superposed, and the small pair is always on the same side of the stem. A similar differentiation has been observed in some European species of *Sphenophyllum*.

We will now go on to describe the internal structure. The anatomy of the stem is exceedingly remarkable, and quite unlike that of the stem in any other group of plants. It was made known, in the first instance, by the investigations of M. Renault[1] on the French specimens. This observer was so fortunate as to find the internal organisation preserved, in specimens which at the same time showed the external characters of definite species, and this is one reason why *Sphenophyllum* has become one of the best-known fossil genera. One anatomical feature is constant in all the forms examined. We always find, in the middle of the stem, a solid strand of primary wood without pith, and this strand is either triarch or hexarch in structure, and was always centripetally developed, as shown by the position of the spiral elements at the prominent angles (see Figs. 36-38, 40, and 41, B).

First of all, we will confine ourselves to the primary structure, as shown, for example, in the species from the Lower Coal-measures of Lancashire and Yorkshire, named *Sphenophyllum plurifoliatum*[2] (Figs. 37 and 38). The primary wood, as seen in transverse section, is triangular; it consists entirely of tracheae, without pith or conjunctive parenchyma. At the angles, narrow spiral or reticulate elements are found, marking, no doubt, the starting-points of the development. The more internal part of the wood consists of large, pitted tracheae. In this case the structure is clearly triarch, like that of so

[1] See his *Cours de botanique fossile*, vols. ii. and iv., and the earlier papers there cited.

[2] See Williamson and Scott, "Further Observations on the Fossil Plants of the Coal-measures," Part i., and the earlier memoirs of Williamson, there cited.

many roots; such a structure is very rare in stems, though we find an example in the smaller branches of *Psilotum*. In some French species of *Sphenophyllum*,

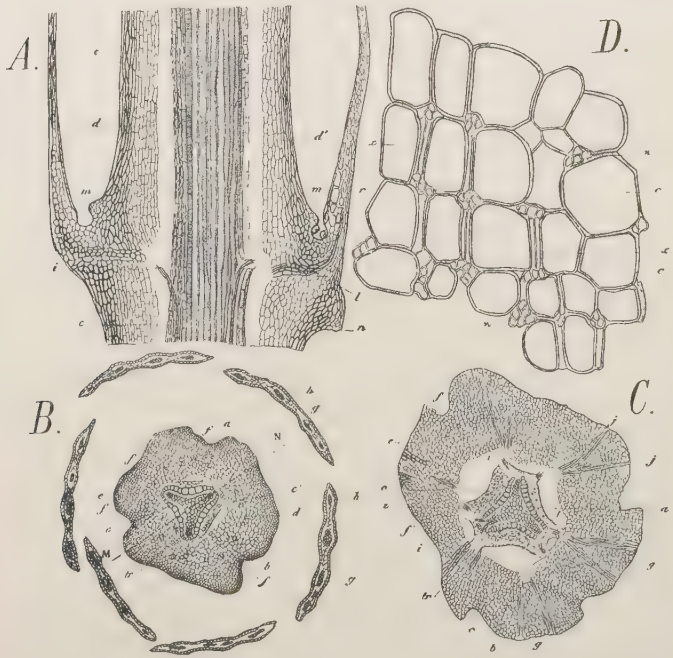

FIG. 36.—*Sphenophyllum quadrifidum*. A. Radial section through a node, showing leaves, cut in the plane MN of Fig. B. In the middle is the stele, showing primary and secondary wood. *c'*, phloëm; *d'*, inner, *e*, outer cortex; *i'*, leaf-trace; *l*, base of leaf; *m*, axillary bud (?); *n*, cortical emergence below node. B. Transverse section of same stem, a little above node, showing six leaves surrounding stem. *a*, *b*, primary wood; *tr*, protoxylem; *c*, secondary wood; *c'*, phloëm; *d*, *e*, cortex; *f'*, furrows; *g*, *h*, leaves, each with four vascular bundles. C. Transverse section through a node, showing the forking leaf-trace bundles, *j*, *j*. Other lettering as before. A, B, C × 9. D. Transverse section of a portion of secondary wood. *c*, tracheides; *x*, parenchyma between them. The radial direction is vertical in this figure. × about 60. All after Renault.

described by M. Renault, the protoxylem-groups are double,[1] so that here the wood may be described as

[1] The scale of Fig. 36, B and C, is too small to show this point. Cf., however, Fig. 41, B.

hexarch, though the triangular sectional form is retained. In the young specimens but little remains of phloëm have been found; the inner layers of the cortex are of delicate tissue, but towards the outside is a fibrous zone (Fig. 37). The external outline of the cortex, as seen in transverse section, is characteristic, for there

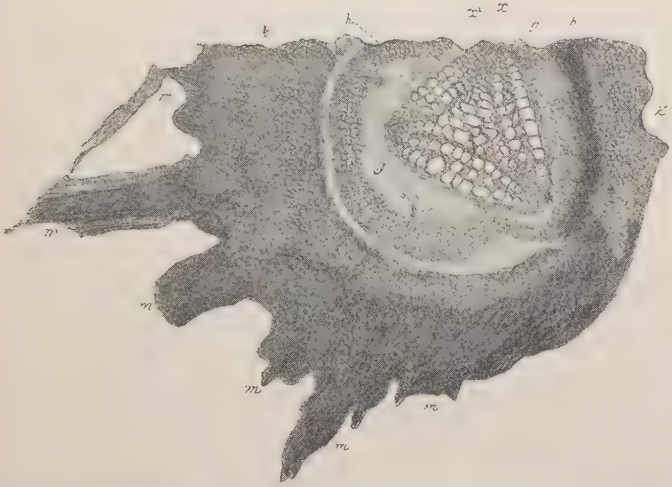

FIG. 37.—*Sphenophyllum plurifoliatum*. Transverse section through whorl of leaves, *m*. *x*, primary wood; x^2, secondary wood; *g*, phloëm (?); *h*, periderm; *k*, outer cortex. × about 20. After Williamson, *Phil. Trans.* Will. Coll. 874.

are three well-marked furrows, lying opposite the three flat sides of the triangular stele (see Fig. 36, B).

It is only in the most minute specimens that the primary structure just described is found unaltered.[1] At a very early stage the formation of secondary wood and bast, by means of a normal cambium, began (Fig. 37). The secondary wood possesses some very

[1] See Fig. 36, B and C, where only one layer of secondary wood is shown. Cf. Fig. 41, B.

remarkable characteristics. It consists of radial series of tracheae, of large size, with numerous bordered pits, chiefly on the radial cell-walls (Fig. 39). Between these tracheae, which, as seen in transverse section, appear square with truncated angles, we find little groups of

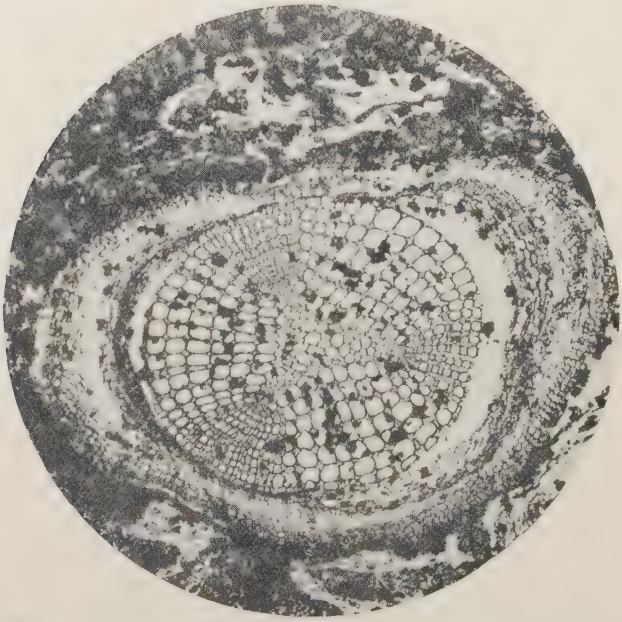

FIG. 38.—*Sphenophyllum plurifoliatum*. Transverse section of older stem, showing triangular primary wood, broad zone of secondary wood, remains of phloëm, and thick periderm; primary cortex cast off. × 18. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 899.

thin-walled cells, fitting into the spaces at the corners (see Fig. 36, D). These represent vertical strands of parenchyma, which are not isolated, but are connected with one another, in the radial direction, by horizontal cells or strands of cells, which are usually quite short, not forming continuous medullary rays (Figs. 36, D, and

39. This peculiar structure of the wood is found both in the English (Figs. 38 and 39) and in the French forms (Fig. 36, D), but is not common to the whole genus, as we shall see presently. The elements of the wood are arranged with the greatest regularity (Fig. 38). There is a marked difference in size between the secondary elements found opposite the sides of the primary wood, and those corresponding to its angles; the former are much the larger (see Fig. 38). In the small-celled wood opposite the angles there is an approach to the formation of continuous rays.

Fig. 39.—*Sphenophyllum plurifoliatum.* Radial section through part of secondary wood, showing pitted tracheides and parenchyma (*r*). × 50. *Phil. Trans.*, W. and S. Will. Coll. 884.

In the best-preserved specimens we find, immediately beyond the wood, the delicate tabular cells of the cambium itself, sometimes most distinctly shown, and beyond this we come to a zone of thin-walled radially-arranged tissue, which can only be interpreted as the phloëm (see Fig. 38).[1] Beyond this again, in older stems, lies a wide band of firmer tissue, also radially arranged, which we must regard as internal periderm (Fig. 38). If we examine a comparatively young stem of *Sphenophyllum*, we find, in many cases, a very distinct beginning of periderm-

[1] For more complete illustrations of the various tissues, see Williamson and Scott, *l.c.*

formation in the inner cortex (Fig. 37, *h*). In older stems, the primary cortex had been cast off altogether. Sometimes traces of its disorganised tissues remain, but ultimately the primary cortex was replaced by a regular scale-bark, formed by successive layers of periderm (Fig. 38). This formation cut deeper and deeper into the cortex, until it reached the phloëm itself, just as in an oak-tree, for example, at the present day. So it appears that the secondary tissue lying outside the wood consists in its inner part of the phloëm, and in its outer part of the periderm, which was formed by a phellogen, arising first in the cortex and afterwards in the phloëm itself.

The species *Sphenophyllum plurifoliatum* is based on petrified specimens; it is not improbable that it may prove to be identical with the contemporary *S. myriophyllum*, Crépin, known in the form of impressions. The species agree in the large number of linear leaves or leaf-segments in a verticil, and in the large diameter (about 1 cm.) attained by the main stems.[1]

I must now say something as to another form of *Sphenophyllum*, known by the name of *Sphenophyllum insigne*. This species was described by Dr. Williamson as long ago as 1874. It is a very interesting form, because it comes from some of the oldest Carboniferous strata, namely from the Burntisland beds, belonging to the Calciferous Sandstone series, at a horizon far below the Coal-measures. In this species, the stem attains a diameter of almost a centimetre—a rather large size for a *Sphenophyllum*. In its general anatomy, the stem,

[1] See Zeiller, *Bassin houiller de Valenciennes, Flore fossile*, p. 422, Pl. lxii. Figs. 2-4.

which has been found at all stages of growth, is like that of the former species, but there are some not unimportant differences of detail. At each of the three

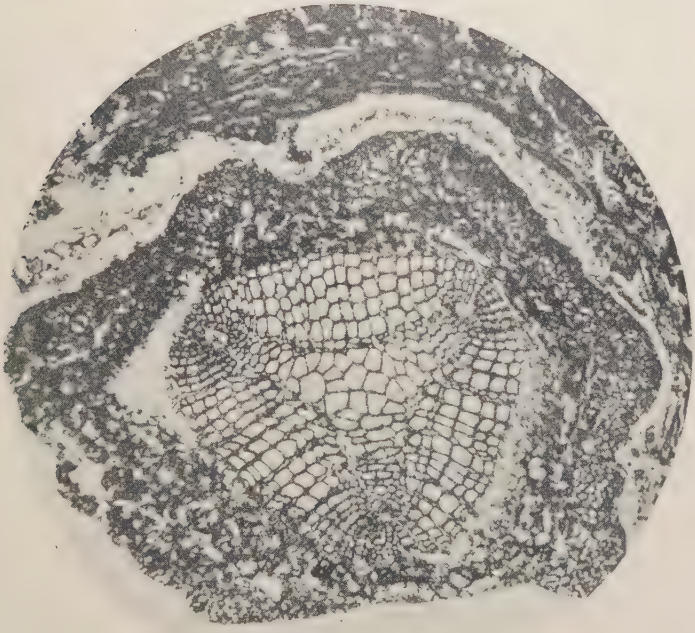

Fig. 40.—*Sphenophyllum insigne*. Transverse section of rather young stem, showing triangular primary wood, with a canal at each angle, marking the protoxylem, then secondary wood, remains of phloëm, and the primary cortex, showing two of the furrows. × about 30. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 919.

angles of the primary wood is a canal, formed, no doubt, in consequence of the disorganisation of the primitive tracheae (Fig. 40). The tracheae generally have a scalariform sculpturing, instead of the numerous rows of bordered pits characteristic of other species. A still

more important difference is the constant presence, in *S. insigne*, of continuous medullary rays, which replace the complicated system of vertical and radial parenchymatous strands in the species above described. In these latter points the Burntisland species differs, not only from *S. plurifoliatum*, but from all other species of *Sphenophyllum* of which the structure is known. For these reasons, and because the older specimens, which have lost their primary cortex, present a very root-like appearance, several palæobotanists disputed the identification of the fossil as a *Sphenophyllum*, imagining that it might be a root of a Cycad or of some unknown plant. The discovery of younger plants, still retaining their cortex (Fig. 40) and nodes, and even portions of the leaves, has completely removed these doubts, and justified Williamson's original opinion.[1] The same species has now been found in the Lower Carboniferous of Silesia, of an age comparable to that of the Scotch specimens. In some specimens of *Sphenophyllum insigne*, the phloëm is remarkably well preserved, and large elements, much resembling the sieve-tubes of some recent Cryptogams, are present.

It is a fact of interest that this, the oldest known *Sphenophyllum* with structure, presents a less peculiar organisation than the forms from later deposits. This fact would seem to indicate that the remarkable arrangement of the wood-parenchyma in the latter species is a later modification, and not a primitive character of the group. Although the near affinities

[1] Williamson and Scott, *l.c.*, p. 926. Williamson's original description is in Part v. of his "Organisation of the Fossil Plants of the Coal-measures," *Phil. Trans.* 1874.

of *S. insigne* with *Sphenophyllum* are now clearly established, it is possible that its anatomical characteristics may ultimately justify its *generic* separation.

Now that we have dealt sufficiently with the morphology and anatomy of the stem, the organisation of the leaves and roots remains to be considered, before going on to the organs of fructification. I have already mentioned that the leaves of *Sphenophyllum* are whorled, and that they vary very much in form, some being broad and wedge-shaped (the type of leaf from which the genus derives its name), while others are deeply divided, or even assume a very simple linear form. It appears to be the rule, that the number of leaves in a whorl was always some multiple of three, a fact which is no doubt correlated with the triarch or hexarch structure of the vascular cylinder. Six was perhaps the most usual number (see Fig. 36, B); but where the leaves were linear this number was considerably increased. In the Coal-measure species, *Sphenophyllum plurifoliatum*, the leaves in each verticil seem to have been eighteen, at least, on the larger stems (Fig. 37). The nodes from which the leaves spring are somewhat enlarged, and the vascular strands pass out almost horizontally (Fig. 36, A). As regards the course of the leaf-trace bundles, our information is chiefly due to M. Renault, who succeeded in working out this question in some of the French forms. In these species, as we have seen above, there are two distinct groups of spiral elements at each angle of the stele—six such groups in all. At the node, one bundle starts from each of these groups, dividing, as it passes through the cortex, into two, three, or four branches, which supplied the

various veins of the leaf (Fig. 36, C). Further division of the bundles took place within the leaf itself, as it widened out, or divided into segments. Where the leaves were linear, the course of the bundles was the same, but in this case each leaf received a single strand only, as in the British species, *S. plurifoliatum*. Numerous vascular bundles, apparently equal in number to the leaves in a whorl, have been found in this species in the outer cortex of the node. They no doubt arose, here also, from the subdivision of a smaller number of strands, given off from the angles of the stele. The branching of the leaf-traces within the cortex is very characteristic of *Sphenophyllum*.

The anatomical structure of the leaf was fully worked out by Renault. The vascular bundles are small and simple, apparently of the concentric type. The tissue of the leaf was strengthened by bands of sclerenchyma, lying next the epidermis of the upper and lower surfaces. The parenchyma is uniform throughout. There is thus nothing remarkable in the anatomy of the leaf, unless it be the strong mechanical construction, a point of some interest, for it seems to show that these leaves could not have been floating, as some botanists have assumed, though with but little reason. The narrow, unifascicular leaves or segments of *S. plurifoliatum* had a rather simpler structure.

The roots have also been investigated by Renault. The specimens which he examined were of diarch structure, with secondary wood, resembling that of the stem. Somewhat similar structures are occasionally found in association with the Burntisland *Sphenophyllum* (*S. insigne*), and with the Coal-measure species, *S. pluri-*

foliatum, and were probably the roots of those species. As regards the insertion of the roots, we do not know any details, but they appear to have been borne on the nodes.

2. *Fructifications of Sphenophyllum—S. Dawsoni Type.*—We now come to the question of the fructification of *Sphenophyllum*, our knowledge of which has grown rapidly during the last few years. Our first accurate information, with regard to the fructification of the genus, depended on the observations of Williamson, who described in the greatest detail a fructification which has since been proved to be that of a species of *Sphenophyllum*, named provisionally *S. Dawsoni*. We are now, however, acquainted with four distinct types of fructification in *Sphenophyllum*, on which a subdivision of the genus will no doubt ultimately be based.

We will begin with the description of the type of cone investigated by Williamson, with which, as M. Zeiller has shown, the fructifications of the well-known species *Sphenophyllum cuneifolium* agree in all essential respects.[1] The British specimens, which come from the calcareous nodules of the Lower Coal-measures, show the internal organisation in great perfection,[2] while

[1] Zeiller, "Étude sur la constitution de l'appareil fructificateur des Sphénophyllum," *Mém. de la Soc. géol. de France*, "Paléontologie," Mém. 11, 1893.

[2] Williamson first described his specimens under the name of *Volkmannia Dawsoni*, using a generic name of very indefinite signification, and subsequently called them *Bowmanites Dawsoni*. The name *Bowmanites* (a genus founded in 1871 by Binney) is still retained for fructifications of Sphenophylleae, but, as we have some evidence in this case as to the vegetative structure, it is simpler to call Williamson's specimens *Sphenophyllum Dawsoni*—a name which may turn out to be synonymous in part with *S. cuneifolium*. See Williamson, "On the Organisation of an

those of the French observer, which are preserved in the form of impressions, give an excellent idea of the external characters, and afford the proof that these cones were really borne on *Sphenophyllum* stems. It appears that under the type-name *Sphenophyllum Dawsoni* two forms are included, the larger of which is probably identical, as M. Zeiller believed, with *S. cuneifolium*, while the smaller may represent the fructification of *S. plurifoliatum* (= *S. myriophyllum* ?). The following description applies, except when otherwise stated, to the larger species, which may be distinguished provisionally as the *a* form.

In external aspect, the cones, which reach a length of several inches, with a diameter of half an inch or more, are not unlike some of the Calamarian fructifications (see Fig. 35). The free surface of the cone is formed by the upturned tips of the whorled bracts. The arrangement of the organs, as shown in *Sphenophyllum Dawsoni*, and illustrated by the diagram, Fig. 41, A, is as follows: the cone has an axis 2-3 mm. in diameter, bearing at intervals numerous whorls of bracts; the bracts of each verticil are coherent for a considerable distance from the axis, forming a kind of cup; at the edge of the cup, the individual bracts become free from one another and turn vertically upwards, extending for a distance equal to several internodes, so that the tips of several successive verticils overlap each other (cf. Figs. 41, A, and 42). The number of bracts in each whorl varies, ranging from fourteen to about twenty in the

undescribed Verticillate Strobilus, etc.," *Manchester Lit. and Phil. Soc.* 1871; "Organisation of Fossil Plants of the Coal-measures," Parts v. (1874) and xviii. (1891); Williamson and Scott, *l.c.*

cases where it was possible to count them. It has not yet been decided for certain whether the bracts of successive whorls were alternate or superposed; though the

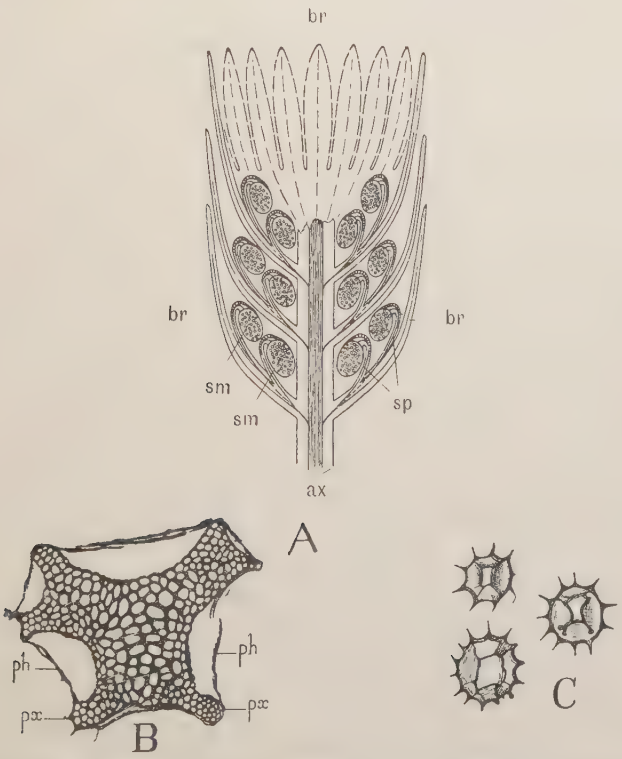

FIG. 41.—*Sphenophyllum Dawsoni*. A. Diagram of cone in longitudinal section, showing three whorls. *ax*, axis; *br*, bracts; *sp*, sporangiophores; *sm*, sporangia; *br'*, whorl of bracts seen from the inside in surface view. (G. T. G.) B. Stele of axis, in transverse section. Wood only preserved. *px*, protoxylem-groups, of which there are six in all; *ph*, remains of phloëm. × about 20. Will. Coll. 1049. C. Spores, in superficial aspect. × about 100. B and C after Williamson, *Phil. Trans.*

analogy of the vegetative leaves would lead one to expect superposition, the direct evidence is in favour of an alternate arrangement. The sporangia were

borne singly on long pedicels or sporangiophores, which sprang from the upper surface of each verticil of bracts in its united part, near the axis (Fig. 41, A, *sp*, Fig. 42, B and C). The pedicels are generally twice as numerous as the bracts; they are ranged in a single whorl, but are of unequal lengths, so that the sporangia of the same whorl overlap each other (Fig. 42). This gives the impression that more than one verticil of sporangiophores may spring from a single whorl of bracts, but this is not the case, though the point at which the sporangiophore becomes free from the bract is variable.

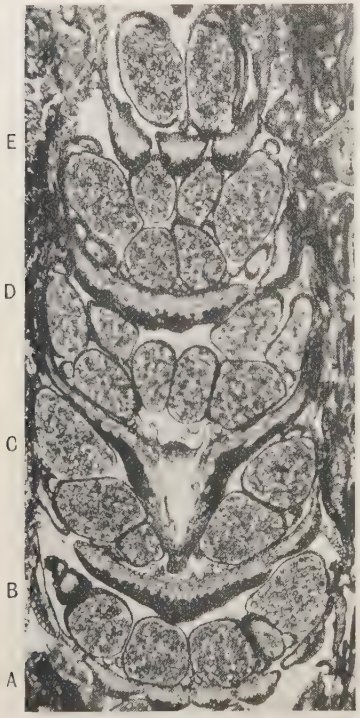

FIG. 42.—*Sphenophyllum Dawsoni*, β. Somewhat oblique longitudinal section of cone, mostly tangential, but passing through axis below C, where the bracts are connected with the axis. Five verticils (A-E) are shown. At B and D the bracts are connate; at A and E they have separated; at B and C the attachment of sporangiophores to bracts is shown; at E, especially to the right, the relation of sporangiophore to sporangium is very clear. × 9. From a photograph by Mr. Lomax. University College Collection, EE, i, c.

The pedicel is a slender stalk, becoming rather thicker near the top, where it bends over towards the axis of the cone, and bears a single pendulous sporangium. The position of the sporangium on its pedicel is much like that of an anatropous ovule in relation to its funiculus (cf. Figs. 41, A, 42, E, 43, and 44).

We have now gained some idea of the general morphology of the cone, the chief points in which are the gamophyllous verticils of sterile bracts, and the sporangiophores, twice as numerous as the bracts, springing from their upper surface, and bearing each a single pendulous sporangium at the end. The complex structure of the whole strobilus is well shown in the transverse section, Fig. 43, from one of Williamson's drawings, and in the longitudinal section, Fig. 42.

We will now go on to describe the structure more in detail. In some specimens of *S. Dawsoni* the axis is well preserved; it is traversed by a triquetrous strand of solid wood, without pith (Fig. 41, B), like that of the vegetative stem in other species of the genus. It was this anatomical similarity which first led Williamson to regard his specimens as akin to *Sphenophyllum*, long before Zeiller's observations proved their identity. In *S. Dawsoni*, form *a*, the corners of the wood are truncated, or even widely forked, and there were two strands of primitive tracheae to each (Fig. 41, B, *px*), so that the whole stele was hexarch,[1] as in some French species. Associated with the cones of *S. Dawsoni* a single fragment of a vegetative stem has been found, showing a primary structure just like that of the axis of the strobilus, but with the addition of a broad zone of secondary wood and bast. There can be little doubt that this specimen represents the vegetative stem of *Sphenophyllum Dawsoni*, form *a*, and if so, that species was evidently distinct from any other *Sphenophyllum* of which the structure is known, though probably identical

[1] Owing to irregularities in the forking, the stele sometimes appears pentarch.

with *S. cuneifolium*. In the smaller form (β) there is a slender, triarch xylem.

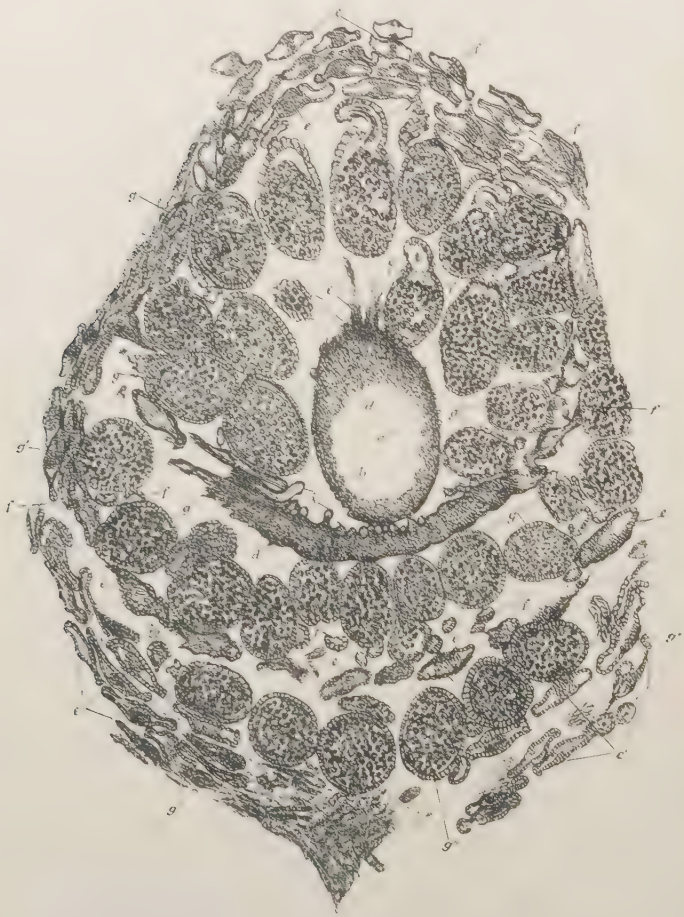

FIG. 43.—*Sphenophyllum Dawsoni*, *a*. Obliquely transverse section of cone, showing parts of three whorls of bracts. *a''*, hollow axis (stele missing); *b*, *d*, cortex of axis; *e*, *e'*, bracts cut at different levels; *f*, sporangiophores, the innermost just springing from a whorl of bracts, which are here coherent; *f'*, sporangiophores in connection with their sporangia; *g*, *g'*, *g''*, sporangia of the three whorls. × 7. After Williamson, *Phil. Trans.* Will. Coll. 1049 B.

In the axis of the cone we find that the cortex, so far as it is preserved, resembles that of a young vegetative stem. The course of the vascular strands supplying the bracts and sporangiophores has been, to some extent, traced; the bundles given off from the central cylinder underwent much subdivision in passing through the cortex, until they were equal in number to the bracts in a verticil. The most interesting point is, that each of these strands, immediately on entering the verticil, divides into three branches, one of which lies below the other two. The lower branch passes through the coherent whorl and out into the free tip of the bract to which it belongs; the two upper branches of the strand pass out into the pedicels of the two sporangiophores corresponding to the bract in question (see Fig. 41, A, *sp*). Thus we see that by anatomy, as well as position, the sporangiophores are shown to be appendages of the bract from which they arise.

The bracts themselves are of simple structure (Figs. 42, 43); the epidermis contains stomata, similar to those of some Ferns. The slender vascular bundle extends right through the bract.

The sporangiophores either separated from the whorl of bracts as soon as the latter became free from the axis, or remained adherent for some distance to their upper surface; the vascular strand in each sporangiophore traversed the whole length of the pedicel, increasing in thickness towards the top, and eventually ending suddenly at the base of the sporangium (see Fig. 43, *f'*; Fig. 44). In the upper part of the pedicel, and especially where it bends over

towards the axis, the epidermal cells are much enlarged, and these large cells of the pedicel are continuous with those that form the wall of the sporangium itself (Figs. 43 and 44). Towards the free end of the sporangium, the cells of the wall become much smaller, and it was probably at this end that dehiscence took place, the large cells perhaps performing the functions of an annulus. These cells were strengthened by buttresses projecting from their lateral cell-walls, much as in the sporangium of *Calamostachys*. The sporangium is seated, with a broad base, on the recurved end of the pedicel; the sporangial wall in this region is lined by a delicate tissue (Fig. 44).

FIG. 44.—*Sphenophyllum Dawsoni*. Sporangiophore and its sporangium, shown in transverse section above, and in longitudinal section (somewhat oblique) below. *sp*, sporangiophore; *sm*, sporangium, containing spores. × 45. *Phil. Trans.*, W. and S. Will. Coll. 1898, H. and E.

The spores were numerous in each sporangium, and so far as at present observed, were all of one kind, though rather variable in size. Their average diameter is about .09 mm. The spore-membrane shows a characteristic sculpturing, consisting essentially of prominent spines, connected

together by a network of elevated ridges or wings (see Fig. 41, C).

The above description, based on the *Sphenophyllum Dawsoni* of Williamson, is now known to hold good, in all essential points, for *Sphenophyllum cuneifolium*, with which, indeed, M. Zeiller, to whom we are indebted for a most minute comparison of the two cones, thinks it identical; this conclusion is probably correct as regards the larger form of *S. Dawsoni*. Several species, in addition to *S. cuneifolium*, were examined by M. Zeiller, and in these also he was able to show that the sporangia were borne on pedicels, arising from the upper surface of the bracts.

So many specimens of *S. Dawsoni*, all showing spores of the same kind, have now been investigated that there is little doubt that these cones were homosporous. A specimen described many years ago by M. Renault, and supposed to show heterospory, is now admitted to have been wrongly interpreted; the structure which was formerly regarded as a megaspore is in reality nothing but a fragment of tissue, probably forming part of the wall of a sporangium.

The occurrence of spores of somewhat different dimensions in adjacent sporangia (averaging .083 mm. in one sporangium, and .106 mm. in another), those of the larger size being accompanied by minute, presumably abortive spores, has recently been interpreted as a possible indication of incipient heterospory.[1]

3. *Bowmanites Römeri*, *Sphenophyllum fertile*, and *S. majus*.—About twelve years ago the investigations of

[1] Thoday, *New Phytologist*, vol. v., April 1906.

Count Solms-Laubach made us acquainted with a fructification, of the *Sphenophyllum* type, which differs in important respects from those already described. The author named his specimen *Bowmanites Römeri*,[1] using the generic name *Bowmanites* to include all fructifications referable to the family Sphenophylleae.[2] This nomenclature is the most suitable in this case, for, in the absence of any vegetative organs, we cannot be certain that the specimen belonged to a member of the genus *Sphenophyllum*, though most probably this was the case. *Bowmanites Römeri* is at present only known from a single fragment, happily very well preserved, from the Coal-measures of Cracow. The axis is not present, but the arrangement and structure of the bracts and sporangia have been made clear by the researches of the discoverer. The bracts are in whorls, and those of each whorl are united towards the base, though not for so long a distance as in *Sphenophyllum Dawsoni*; the bracts are directed steeply upwards, and several successive verticils overlap each other. In this case it seems to be proved that the members of successive whorls were superposed, like the foliage-leaves of *Sphenophyllum*. The structure of the bracts is similar to that in *S. Dawsoni*; each is traversed by a single vascular bundle. (See Fig. 45, for an outline transverse section of half the strobilus.)

The point of chief interest is the position of the sporangia, two of which were borne on each sporangiophore. The pedicel expanded at the top into a scale

[1] "*Bowmanites Römeri*, eine neue Sphenophylleen-Fructification," *Jahrbuch der k. k. geolog. Reichsanstalt*, Vienna, 1895.

[2] The appropriate but, as the author allows, sesquipedalian name, *Sphenophyllostachys* has been introduced by Prof. Seward in the same sense.

of considerable size (Fig. 46, A), from which the two sporangia hung down side by side, towards the axis of the cone.[1] It appears that the pedicels in this species were short, and that they were arranged in three concentric verticils, on each whorl of bracts—another apparent difference from *Sphenophyllum Dawsoni*. The pedicel, which much resembles a sterile bract in structure,

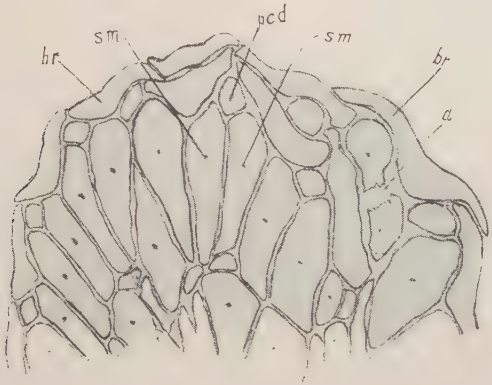

FIG. 45.—*Bowmanites Römeri*. Part of transverse section of cone. *br*, bracts; *pcd*, pedicel of sporangiophore; *sm*, the two sporangia belonging to it. At *a* the lamina of a sporangiophore is shown. × 10. After Solms-Laubach.

is traversed by a vascular bundle, which, where it enters the scale at the top, divides into two branches to supply the two sporangia (Fig. 46, A). The anatomical structure of the sporangiophore, allowing for the greater size and complication associated with the presence of two sporangia instead of one, closely resembles that of *Sphenophyllum Dawsoni* (Fig. 46). The sporangium has a wall several cells in thickness; in *S. Dawsoni* this is

[1] In the transverse section (Fig. 45) the pairs of sporangia (*sm*) are shown, with the pedicel (*pcd*) between the two sporangia, and on their outer side.

only the case at the base, but the difference may be merely a matter of preservation. The spores in each sporangium are numerous, and closely resemble those of *Sphenophyllum Dawsoni*, the resemblance extending

FIG. 46.—*Bowmanites Römeri*. A. Lamina of sporangiophore, cut nearly parallel to its upper surface, and above the insertion of the sporangia. *v.b.*, vascular bundle. B. Longitudinal section through upper part of sporangiophore, showing insertion of sporangium. *ped.*, pedicel; *sm*, part of sporangium; *s*, spores. × about 60. After Solms-Laubach.

to the most minute details of structure of the spore-membrane.

There can be no doubt that this discovery of Count Solms-Laubach's threw a great light on the morphology

of *Sphenophyllum*. In particular, the structure of the complex sporangiophores, each bearing two sporangia, showed that these organs cannot be regarded as mere sporangial stalks, but that they are rather comparable to the peltate scales of the Equisetales. At the same time, their structure and position go far to confirm Zeiller's opinion that the sporangiophores of Sphenophylleae may be interpreted as ventral lobes of the leaf, the bract itself representing the dorsal lobe. On all these points much further light has been thrown by the still more recent discovery of other new types of fructification, now to be described.

A recently discovered fructification (*Sphenophyllum fertile*, Scott [1]) from the Lower Coal-measures of Shore Littleborough, in Lancashire, resembles *Bowmanites Römeri* in having peltate, bisporangiate sporangiophores, but is peculiar in the fact that both the dorsal and ventral lobes of the sporophyll are fertile; the sterile bracts, which in other Sphenophyllaceous strobili represent the dorsal lobes, are here replaced by additional sporangiophores. The sporophyll is also more complex than in other species, its lobes, both dorsal and ventral, dividing in a palmate manner into several branches, each of which constitutes a sporangiophore (Fig. 47). The anatomy of the axis of the cone is in all respects that of a typical *Sphenophyllum*, so that in this case there can be no doubt as to the attribution of the fructification.

It is only in a few cases, of which the three types already described are the chief, that the preservation of

[1] Scott, "On a New Type of Sphenophyllaceous Cone (*S. fertile*) from the Lower Coal-measures," *Phil. Trans. Roy. Soc.* B, vol. 198, 1905.

structure enables us to clearly understand the organisation of Sphenophyllaceous strobili. Specimens preserved only as carbonaceous impressions may, however, afford

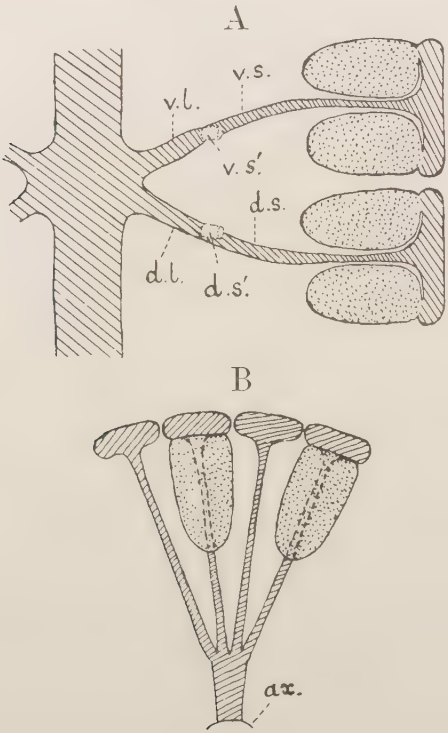

FIG. 47.—*Sphenophyllum fertile*. Diagram A. Node in radial section, showing one sporophyll. *v.l.*, ventral lobe; *v.s.*, a ventral sporangiophore bearing two sporangia; *v.s'.*, stump of another sporangiophore; *d.l.*, *d.s.*, *d.s'.*, corresponding dorsal parts. B. one lobe of sporophyll, as seen in a transverse section of the cone; *ax*, axis. On two of the sporangiophores a sporangium is shown. From Scott, *Phil. Trans.*

suggestive indications, and suffice to show that, within the limits of what we call the genus *Sphenophyllum*, there must have been great variety in the fructification. In *S. majus*, for example, the impressions of the lax fertile

spikes show the sporangia grouped in fours, the groups resting on the upper surface of a repeatedly forked bract, below the points of bifurcation (Fig. 48). This form is interesting from its analogy with the fructification of the recent *Tmesipteris*, while in *S. trichomatosum*,[1] on the other hand, the arrangement seems to have been a very simple one, the sporangia appearing to be sessile and solitary on each bract in the axils of the bracts. It is quite possible, however, that a short pedicel was present.

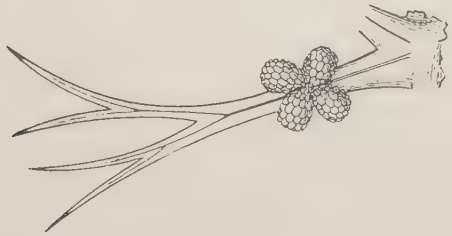

FIG. 48.—*Sphenophyllum majus.* Forked sporophyll bearing four sporangia. After Kidston.

The four most important types of fructification are those of *S. Dawsoni*, *Bowmanites Römeri*, *S. fertile*, and *S. majus*.

It follows sufficiently, from what has already been said, that *Sphenophyllum* represents a perfectly distinct group of plants, of which all the parts—stem, leaves, roots, and fructification—are known in one species or another. There is no longer any room for the idea, once sanctioned by good palæobotanical authorities, that

[1] I am indebted to my friend, Mr. R. Kidston, F.R.S.E., for information as to these species. On *Sphenophyllum trichomatosum*, see Mr. Kidston's paper in *Proc. Royal Phys. Soc. of Edinburgh*, vol. ii. 1891, and on *S. majus* and other species, his Carboniferous Lycopods and Sphenophylls, *Trans. Nat. Hist. Soc. Glasgow*, vol. vi. Part i. 1899-1900.

Sphenophyllum might represent the foliage of some of the Calamites. This mistake arose from the fact that the finely-divided or linear form of foliage, often occurring in species of *Sphenophyllum*, sometimes bears a great external resemblance to the foliage of the branches known as *Asterophyllites*, which really belonged to Calamitean stems. This resemblance may easily lead to confusion, in cases where we have to deal with imperfect specimens without structure, but of course it proves nothing as to any connection between the two groups of plants. External characters of the foliage are as unsafe a guide among fossil as among recent plants. If the genus *Galium* had existed in Carboniferous times, we should no doubt have often been puzzled to distinguish its remains from those of *Sphenophyllum* or of *Calamites*. It is the specimens with their structure preserved which give the only safe clue to the interpretation of the rest. The discussion of the affinities of *Sphenophyllum* will best be postponed until the next family has been considered.

II. Cheirostrobeae

4. *Cheirostrobus*.—This very distinct type of strobilus was originally described from a single specimen of the actual cone, and another fragment containing the peduncle. The specimens, of which two more have since come to light, were derived from the famous deposit at Pettycur, on the Firth of Forth, belonging to the Calciferous Sandstone series, at the base of the Carboniferous formation. The fossil is therefore of great antiquity, and is, in fact, among the oldest

fructifications of which the structure is known. It occurs side by side with the stems of *Sphenophyllum insigne*, from which, however, it differs so much in structure as to preclude all idea of any connection between them.

The structure is admirably preserved, so that the whole organisation of the strobilus could be worked out, though unfortunately nothing is known for certain as to the vegetative organs on which it was borne. The cone was a large one—from 3.5 cm. to 4 cm. in diameter, and certainly exceeding 10 cm. in length. Its whole organisation is exhibited in the diagrammatic sections in Fig. 49. The axis, about 7 mm. thick, bore numerous, crowded verticils of modified leaves or sporophylls, of which there were about twelve in each whorl, the number diminishing towards the apex; the members of successive whorls were accurately superposed in vertical series, as in *Sphenophyllum*. The sporophylls were compound, and indeed remarkably elaborate in form and structure, so much so as to differ widely from any other organs to which the name is applied. The important point is, that in *Cheirostrobus*, each sporophyll was subdivided in two planes; immediately above its base it branched into an inferior and a superior lobe, while at the same time both lobes subdivided, in a palmate manner, into segments. The total number of segments was usually six, of which three belonged to the lower lobe, and three to the upper, the latter lying directly above the former (see diagram, Fig. 49). The sporophyll attained a length of 1.4 cm. or more, almost the whole of which was occupied by the free segments, for the common basal

portion was quite short. The general direction of the whole organ was horizontal (see diagram, Fig. 49).

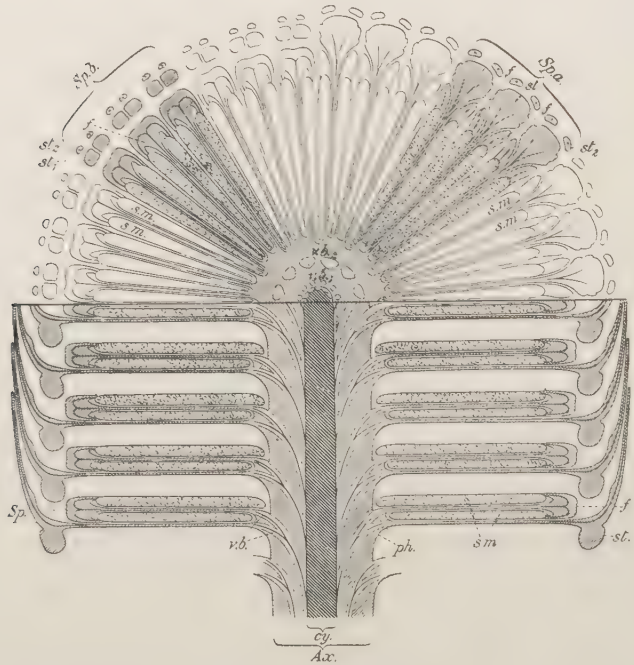

FIG. 49.—*Cheirostrobus pettycurensis*. Diagram. The upper part in transverse, the lower in radial section; the position of the organs corresponds in the two sections.

1. Transverse section. Six complete sporophylls, each with three segments, are shown. *Sp.a.*, section passing through *sterile* segments; *Sp.b.*, do. through *fertile* segments or sporangiophores; *st*, lamina of sterile segment; st_1, downward outgrowths of sterile laminae, cut transversely; st_2, their apices, transverse; *f*, peltate sporangiophores; *sm*, sporangia. Note that in *Sp.a.* each peltate lamina, *f*, is seen in two distinct lobes, with the sterile lamina between. $v.b._1$, $v.b._2$, vascular bundles of two whorls.
2. Radial section. The sporophylls are separated from one another for clearness' sake; in nature they are in close contact. *Ax.*, axis of cone; *cy*, its stele; *ph*, base of sporophyll. Other lettering as in transverse section. The diagram is true to nature as regards proportions of parts, as well as their relative position. × about 2. *Phil. Trans.*, S.

The segments of each sporophyll were of two kinds, the one set fertile, bearing the sporangia, the other

sterile; the three superior segments were the fertile sporangiophores, while the three inferior members were sterile bracts.[1] The two kinds of segments resemble each other in their stalks, which are long and slender in both, but differ in the form of the laminae in which they terminate at their distal extremities.

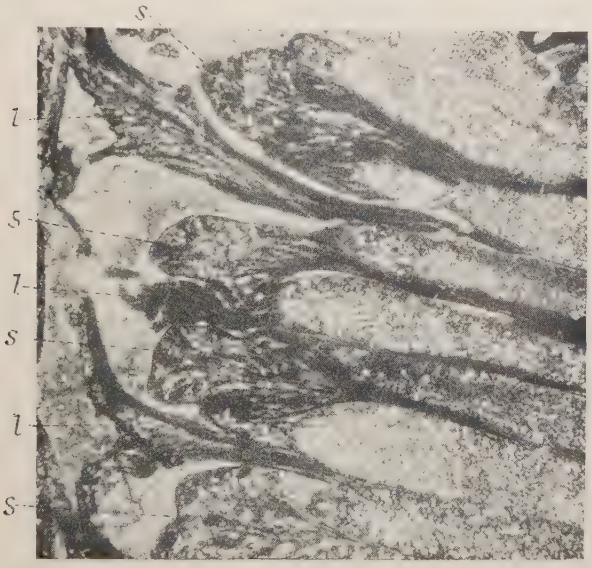

FIG. 50.—*Cheirostrobus pettycurensis*. Part of radial section, showing the peltate sporangiophores, *s*, with the foliaceous sterile segments, *l*, between them. The lowest sterile segment shows the form of the lamina well. The sporangia are seen to the right. × about 10. *Phil. Trans.*, S. Kidston Coll. 87.

The fertile segments or sporangiophores had each a thick peltate lamina, much like that of an *Equisetum* or *Calamostachys*, bearing four sporangia on its inner side (see Fig. 49, *f*, and Fig. 50, *s*). The sporangia

[1] This latter point was not determined without difficulty, as the same segment can rarely be traced from end to end, but is now settled beyond doubt.

were of great length, extending inwards as far as the axis, parallel to the stalks of the segments, between which they were closely packed (Fig. 49). The sterile segments or bracts were slightly longer than the sporangiophores, so that their laminae overlapped those of the latter. The packing was so close that the fertile laminae were grooved above and below to allow the sterile pedicels to pass through (Fig. 49, *Sp.a, f*). The sterile lamina was itself a complex structure, for it divided into two apical prongs, directed almost vertically upwards, while it was prolonged below into two shorter and stouter outgrowths (Fig. 50, *l*, and Fig. 49, *st*). The whole external surface of the cone was thus effectually protected by this complex system of overlapping laminae. We see then that the complete sporophyll consisted of three lower sterile segments and three sporangiophores above them, each of which bore four sporangia, so that the sporophyll as a whole produced no less than twelve sporangia. As there were eleven or twelve such sporophylls in a verticil, and the verticils were very numerous, the total production of sporangia by a cone of *Cheirostrobus* must have been on a great scale. In each sporangium a vast number of spores were produced, which were all of one kind, so far as the single known specimen shows.

It remains for us to describe the anatomical structure of the strobilus. Its axis was traversed by a central cylinder; the wood, which is alone preserved, had a stellate transverse section, with about twelve prominent angles, corresponding in number and position to the vertical series of sporophylls (Fig. 51, *x*). At these angles the spiral elements are placed, so the development

of the wood was evidently centripetal,[1] as in *Sphenophyllum* or in the Lycopodiaceae. The rest of the tracheae bear multiseriate bordered pits, as is commonly the case in *Sphenophyllum*. There was no

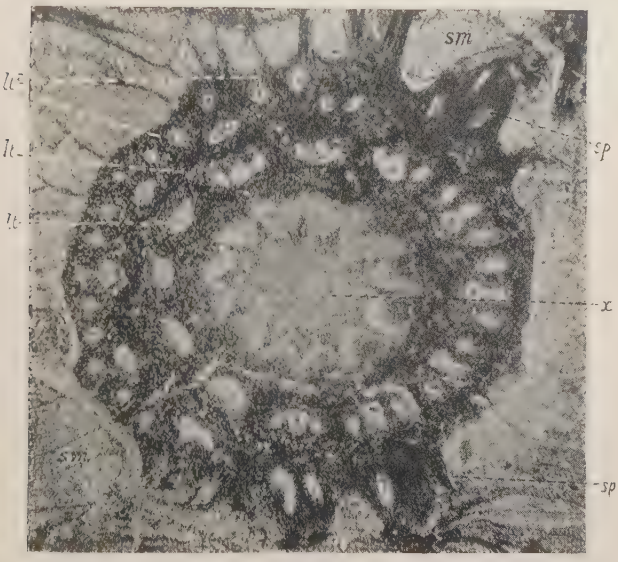

FIG. 51.—*Cheirostrobus pettycurensis*. Transverse section of axis of cone. *x*, xylem with twelve prominent angles; *lt*, leaf-traces, one undivided, the other divided into three; *lt*², leaf-trace, already divided into four bundles, and the inner one subdividing; *sp*, bases of sporophylls; *sm*, sporangia. × about 8. *Phil. Trans.*, S. Kidston Coll. 84 A.

pith, the wood extending to the centre of the stele, though intermixed with conjunctive parenchyma.

The cortex presents no points worth special notice, except that it contained long sacs, perhaps of a secretory nature. The course of the leaf-trace bundles, however, is highly characteristic. They start from the angles

[1] There is some evidence that a minute amount of primary xylem was developed centrifugally.

of the stele, as simple vascular strands, each of which ultimately supplies one sporophyll. When about one-third of the way through the cortex the trace divides into three bundles, a median and two smaller lateral strands (see the *triple* bundle *lt* in Fig. 51). A little further out the median bundle branches again, but this time in a plane at right angles to the first division, so that one of its branches lies above and inside the other (see Fig. 51, on right;[1] also diagram, Fig. 49, *v.b.*). The upper median bundle next divides into three, just as the main strand had previously done, so that now there are six bundles altogether, constituting each leaf-trace, three above and three below; all six enter the base of the sporophyll, and pass out into its segments, the three upper strands supplying the three sporangiophores, while the lower three enter the sterile leaflets (Fig. 49).

The bundle of the sporangiophore, on reaching its peltate lamina, divides into four branches, which run out to the bases of the four sporangia (Fig. 49, *f*). In the sterile lamina the vascular strand divides into two, which enter the two apical points.

The vascular system was thus a highly complex one, corresponding to the great elaboration of the external organisation. Each of the four sporangia of a fertile segment is connected with the peltate lamina by a neck of tissue (Fig. 50, *s*), into which the vascular bundle enters, ending at the base of the sporangium itself. The wall of the latter, which in its actual state of preservation is only one cell thick, consists of long

[1] The reference-line to *x* crosses the median bundles of the trace referred to.

cells, with their lateral membranes stiffened by buttresses, precisely as in a *Calamostachys*. A similar structure occurs, as we have seen, in *Sphenophyllum Dawsoni*. The spores have an average diameter of .065 mm.; their outer membrane is ridged, the ridges apparently corresponding to the lines of junction of the four sister-cells. The specimens known are too few to afford decisive evidence as to whether the plant was homosporous or heterosporous; it is worth noting, however, that the sporangia at the base of the cone show no difference from those borne near the apex, as regards the dimensions of their spores. The peduncle much resembles the axis of the cone itself, but in the peduncle well-marked secondary tissues are present, which in places are well preserved, so as to show the phloëm, and even remains of the cambium, as well as the secondary wood, in which medullary rays can be recognised, separating the rows of tracheae. In one specimen of the cone slight secondary growth had also taken place in the axis.

The cone of *Cheirostrobus pettycurensis* is perhaps the most complex Cryptogamic fructification at present known to us, and it is a striking fact that it should occur at so ancient an horizon as the base of the Carboniferous formation. But, highly modified as it is, *Cheirostrobus* bears the impress of great antiquity in the fact that it is a synthetic type, combining the characters of very different groups of plants. In its peltate sporangiophores, and in the insertion and details of structure of its sporangia, *Cheirostrobus* agrees exactly with the Calamarieae. In the anatomy of the stele, on the other hand, it resembles a Lycopod, of the type of

Lepidodendron, as we shall see in the next chapter. While thus combining certain characters of the Horse-tails and the Club-mosses, *Cheirostrobus* shows the most marked affinities with the Sphenophylleae in the following characters: the arrangement of the appendages in superposed verticils, the palmatifid segmentation of the leaves (sporophylls), the repeated branching of the leaf-traces within the cortex, and the relation of the sporangiophores to the sterile segments or bracts. In *Cheirostrobus* it is evident that the sporangiophores are ventral or superior segments of the same leaf of which the sterile bracts are the dorsal or inferior segments. The same relation holds good for *Sphenophyllum Dawsoni*, and still more clearly for *Bowmanites Kidstoni*, where the homology between sporangiophores and bracts is patent. In fact, this latter species occupies, in this respect, exactly an intermediate position between *Sphenophyllum Dawsoni* and *Cheirostrobus*. *Sphenophyllum fertile*, in which both dorsal and ventral segments are fertile, resembles *Cheirostrobus* in their palmatifid branching. The course of the vascular bundles supplying the sporangiophores and bracts is essentially the same in *Sphenophyllum* and *Cheirostrobus*, though necessarily more complex in the latter.

The general conclusion, to which the various characters point, is that *Cheirostrobus* has more in common with *Sphenophyllum* than with any other group of plants at present known, and that, though the former genus must constitute the type of a distinct family, it is most naturally placed in the same main division of Cryptogams, which we may call the Sphenophyllales.

At the same time, *Cheirostrobus*[1] combines in certain respects the characters of Equisetales and Lycopods. Thus the present genus throws great light on the position of *Sphenophyllum*, which had previously been quite undetermined. We can now scarcely doubt that the Sphenophyllales generally were the highly modified representatives of an ancient stock, with which both Lycopods and Horsetails have affinities.

Pseudoborniales

5. *Pseudobornia*.—Professor Nathorst has recently described a remarkable type of plant from the Upper Devonian of Bear Island in the Arctic Ocean, which may belong to the same stock with the Sphenophyllales. *Pseudobornia ursina*[2] is only known at present in the form of impressions, but the external characters are shown in great perfection. The main stems, believed to have been creeping, attain a diameter of about 10 cm. in their present flattened condition. The stem was articulated and branched; the smaller branches still bear the whorled leaves, of which there appear to have been four in a verticil. The leaves are compound, dividing by repeated dichotomy into several leaflets, each of which is deeply pinnatifid, with numerous fine segments. The isolated leaves were formerly supposed to belong to some unknown group of Ferns. The fructification is in the form of long, lax spikes, bearing

[1] A fuller account of the organisation of *Cheirostrobus* is given in my "Structure and Affinities of Fossil Plants from the Palæozoic Rocks," Part i. On *Cheirostrobus*, *Phil. Trans.* vol. 189, B, 1897.

[2] A. G. Nathorst, "Zur Oberdevonischen Flora der Bären-Insel," *Svenska Vetenskaps-Akademiens Handlingar*, Bd. 36, No. 3, Stockholm, 1902.

whorled sporophylls which resemble reduced vegetative leaves. In the sporangia, borne on the lower part of each sporophyll, indications of probable megaspores have been traced.

Professor Nathorst makes this striking plant the type of a distinct class, the Pseudoborniales, showing affinity with the Sphenophyllales, as well as with *Archaeocalamites* among the Equisetales. The complexity of the leaves suggests a comparison with the compound sporophylls of *Cheirostrobus*, of which the vegetative organs are still unknown, though the fructification of *Pseudobornia* does not favour any near affinity. In *Pseudobornia* we appear to have a new and impressive representative of that ancient synthetic race of plants of which the Sphenophyllales have, until now, formed the only known examples.

CHAPTER V

LYCOPODIALES

Lepidodendron and Lepidophloios

We now come to another of the great divisions of Vascular Cryptogams, that of the Lycopods, or Club-mosses. Here, just as in the case of the Equisetales with which we began, our object, as students of fossil botany, is to extend and deepen our knowledge of a group already more or less familiar to us from our experience of recent plants. We shall find that, as regards the Lycopodiales also, our idea of the Class will become a much more adequate one, when we have made ourselves acquainted with its ancient representatives.

The recent Lycopods are all, in one direction or another, highly specialised forms, with the possible exception of *Phylloglossum*, and even with respect to *Phylloglossum* we are left in some doubt whether its simple organisation may not be due to reduction, rather than to the persistence of primitive characters.

In *Lycopodium* itself, while the external characters are simple enough, we find a singularly complex anatomy of the stem, very different from that of any

other plants, and evidently much modified along peculiar lines of its own.

Selaginella, in a few species (*e.g. S. spinosa*), has a simple and probably primitive anatomical structure, but in a great majority of the forms this has become much elaborated; in a large part of the genus the dimorphic foliage is another mark of specialisation.

The genus *Isoëtes* is clearly a reduced form, and differs in so many points from the rest of the Lycopods, that some doubt has even been cast on its affinity with them, and it is largely by a comparison with fossil types that its position has been re-established.

The Psiloteae, as we shall see in the concluding chapter, appear, in the light of our present knowledge, to be remote from the true Lycopods, and rather to show affinity with the Sphenophyllales.

Broadly speaking, then, we may say that the representatives of the Class now living consist of a number of specialised forms, from which it is not easy to form an idea of the primitive characters of the common stock. The Palæozoic Lycopods throw a new and welcome light on the problem. They were not, it is true, simple forms; like so many other Cryptogams of early periods, they attained in some respects a much higher grade of organisation than their living representatives. Yet, in the ground plan of their structure, the fossil forms probably give us a better idea of the essential characters of the group than any of their recent allies.

1. *Habit.*—We will begin with the great genus *Lepidodendron*, of which more than a hundred so-called species

have been described, according to their external characters. The genus has a wide geological range, first appear-

FIG. 52.—*Lepidodendron elegans.* Restoration of tree, bearing cones. After Grand'Eury, modified.

ing in the Devonian, attaining its maximum in the

Carboniferous period, and dying out, according to our present knowledge, in the Permian. These plants had much the same habit as the *Lycopodia* of the present day, but enormously exceeded them in dimensions, growing into large trees, of which trunks a hundred feet long have been found. The main stem was vertical, rising to a great height before the crown of branches was reached (see restoration, Fig. 52). The ramification was constantly dichotomous; the two limbs of the dichotomy were sometimes equal, as in the forking of the main branches, but were often very unequal; in the latter case the relatively main shoots formed a sympodium, the smaller members of the successive dichotomies simulating lateral branches (Fig. 52). The whole system of ramification was thus an exceedingly complex one, built up of branches of many degrees, and differing much from each other, not only in size, but in structure—a fact which is of great importance in dealing with the comparative anatomy of trunks and twigs.

The young stems and branches were densely clothed with numerous simple leaves of acicular or linear form (Fig. 53), and sometimes of great length, amounting in certain cases to as much as 6 or 7 inches. The phyllotaxis was either a close spiral with some very complex divergence, such as $\frac{89}{233}$, or consisted of a system of whorls, the members of successive whorls having themselves a complicated spiral arrangement.

When the leaves were shed, their bases remained attached to the surface of the stem, forming the leaf-cushions (Fig. 53, A), which were persistent even on the larger trunks. It is chiefly on the superficial

characters, presented by this armature of leaf-cushions, (Fig. 54) that the distinction of species has been

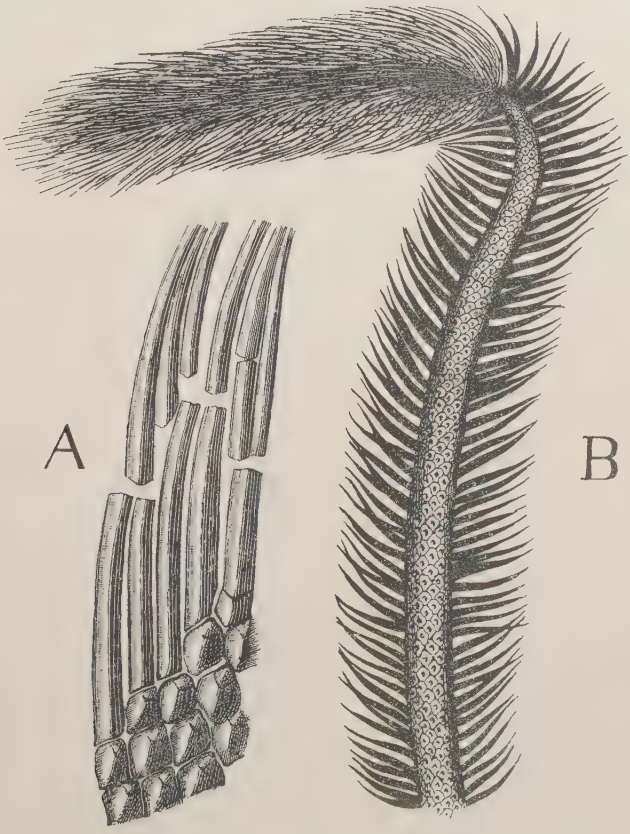

FIG. 53.—*Lepidodendron Ophiurus*. A. Fragment of stem-surface, showing leaf-bases and leaves. B. Leafy branch, bearing a cone at its extremity. Nat. size. After Zeiller.

founded. It will be well to describe in some detail the essential features of the persistent leaf-base.

The leaf-cushions are either packed together quite

closely and separated only by narrow grooves (Fig. 54), or more scattered, with wider flat bands of the

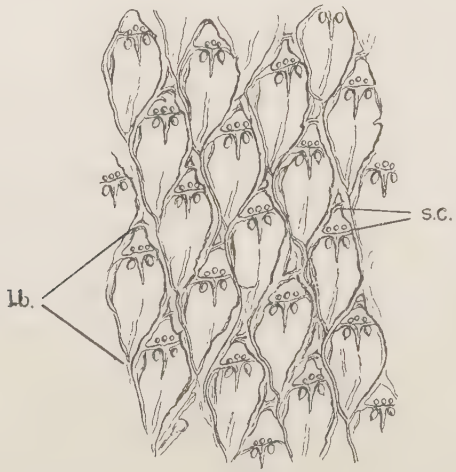

FIG. 54.—*Lepidodendron Veltheimianum*. Portion of surface of stem, showing the leaf-bases (*l.b.*), with the leaf-scar (*s.c.*) at the upper end of each. ¾ nat. size.

stem-surface exposed between them. The whole cushion is rhombic in outline, and somewhat prominent, having a flatly pyramidal form. The apex of the pyramid is truncated, forming a flat surface, which represents the scar left by the fall of the leaf (see Fig. 55, *s.c*). Thus the actual scar only occupies a small part of the whole rhombic area, most of which is formed by the persistent leaf-cushion. The whole is not symmetrical, for the leaf-scar always lies near the upper end of the cushion. On the flat surface of the scar itself, three

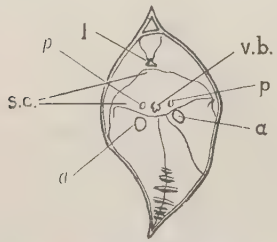

FIG. 55.—*Lepidodendron*. Leaf-base. *sc*, leaf-scar; *v.b.*, print of bundle; *p*, double parichnos; *α*, superficial prints on either side of cushion; *l*, ligule. Figs. 54 and 55 after Stur.

marks or prints are seen, all of which lie in a horizontal line, towards the lower edge of the scar. The anatomy of specimens with their structure preserved has shown that, of these three marks, the median one alone represents the vascular bundle, which originally passed out into the leaf. The two lateral scars, as we shall see presently, represent parenchymatous strands; together they bear the name of the *parichnos*.

Besides the marks on the actual scar, there are others on the surface of the leaf-cushion. The most conspicuous of these are two large round prints or depressions below the scar, lying one on each side of the prominent angle of the pyramidal cushion (see Fig. 55, *a*). These, as is shown by anatomical investigation, were connected internally with the parichnos.

Immediately above the scar, and in the median line of the cushion, is a small triangular print (Fig. 55, *l*), which has been proved to mark the position of the *ligule*; in *Lepidodendron* this organ was constantly present on the upper side of the leaf-base, as in the genera *Selaginella* and *Isoëtes* at the present day. Other marks are sometimes found on the leaf-cushions, but those already described are the most constant and important.

The above description is based on the most perfect specimens preserved as *casts*, *i.e.* with the surface showing its natural form. Where, as is often the case, the specimen represents a "mould" of the exterior, the depressions and elevations are, of course, reversed.

We have a curious illustration of the difficulties of nomenclature in fossil botany, in the fact that distinct genera have been founded on specimens which are now known to represent merely imperfect states of preserva-

tion of various *Lepidodendra*. Thus, when the epidermis had been lost before fossilisation, some of the characteristic markings disappear, or change their form, and we get the so-called genus *Bergeria*. If the destruction had gone a little deeper, removing the outer layers of cortex, the leaf-trace is the only print that remains, and that now lies in the middle of each rhombic area, giving rise to the form called *Aspidiaria*. Lastly, where the whole bark of an old stem had been stripped off, a totally different appearance is produced, resembling an irregularly fluted column. The inclined, overlapping ridges here correspond to the course of the leaf-trace bundles through the middle cortex, and on this state of preservation the genus *Knorria* has, in part at least, been founded.[1]

Leaving these false genera, which are only of botanical interest in so far as they illustrate the difficulties of the subject, we pass on to a group of fossils which are really distinct from, though closely allied to, *Lepidodendron*. This is the genus *Lepidophloios*, typically characterised by the form of the scale-like, imbricating leaf-cushions, which are in most cases transversely elongated, the horizontal diameter exceeding the vertical[2] (Fig. 62, p. 156). The leaf-scar, which bears the usual three prints, is also, as a rule, elongated in the horizontal direction, and of rhomboidal or oval form. Another peculiarity is, that in *Lepidophloios* the leaf-cushions are very prominent, with the pyramidal form much more marked than in *Lepidodendron* (see Fig. 68, B, p. 169). It appears that the leaf-scar was placed towards the

[1] Illustrations of these forms of preservation will be found in Solms-Laubach's *Fossil Botany*, English edition, Figs. 19 and 20.

[2] See Kidston, "On the British Species of the Genus *Lepidophloios*," *Trans. Roy. Soc. Edinburgh*, vol. xxxvii. 1893.

upper side of the cushion in the younger specimens, but that the leaf-bases bent downwards in the older stems, bringing the scar to a lower level (cf. Fig. 63, p. 159). *Lepidophloios* is of interest, though differing so slightly from *Lepidodendron*, because some of the specimens with structure certainly belonged to it, as did also some of the forms to be described further on, in which the probable position of the fructifications on the branches has been determined. So far as is known, however, there is no constant difference in internal structure between *Lepidophloios* and *Lepidodendron*, and in dealing with the anatomy, the latter name will usually be employed, treating *Lepidophloios*, for our present purpose, as a subgenus.

2. *Stem.*—We have now a very considerable mass of material for the study of the internal structure of Lepidodendreae, and of this material the greater part has been derived from the British Carboniferous rocks. Our knowledge of the anatomy of the group is chiefly due to the researches of Williamson, who worked out and described the anatomy of no less than nine distinct forms of the group, though some of these are better known than others. The Continental strata have so far yielded comparatively few specimens of *Lepidodendron*, with structure preserved, so our description will be chiefly based on the British fossils.

The great anatomical feature, which is common to all known stems of *Lepidodendron*, is the presence of a single stele, with centripetally developed primary wood. The occurrence of a pith is inconstant, not only among different species, but even in different

parts of one and the same individual; sometimes (as in the larger stems of most species) the interior of the vascular cylinder is occupied by a medulla, around which the wood forms a continuous ring (Figs. 56 and 58); sometimes the wood constitutes a solid mass extending to the middle of the stele (Figs. 59 and 60). In all cases, the wood of the stem, whether solid or hollow, forms a perfectly continuous cylinder or ring, and is not broken up, as in the higher plants, into distinct vascular bundles. The xylem-cylinder is surrounded by a ring of phloëm (Figs. 57 and 60). From the outer border of the stele, numerous leaf-trace bundles arise, passing out obliquely through the cortex to the leaves, each of which receives a single bundle (Figs. 56 and 59). The cortex is of great thickness relatively to the vascular cylinder. Its structure varies much according to the species, and to the dimensions and age of the branch.

The majority of the British species, in which the anatomy is preserved, are known to have formed a zone of secondary wood and bast, often of considerable thickness, around the primary cylinder. In addition to this growth of the stele, a still more extensive development of secondary tissues went on in the outer cortex, leading to the formation of a thick periderm (Figs. 58 and 59), which seems to have been produced in all the species, even in cases where no secondary vascular tissues have so far been found. The following is a list of the British forms, hitherto described, of which the structure is known :—

I. Secondary Wood not observed

1. *Lepidodendron Harcourtii*, Witham ; Coal-measures.
2. *L. parvulum*, Williamson ; Coal-measures.
3. *L. macrophyllum*, Williamson ; Coal-measures.
4. *L. Hickii*, Watson ; Coal-measures.
5. *L. aculeatum*, Sternb. ; Coal-measures.

II. With Secondary Wood

6. *Lepidodendron brevifolium*, Williamson ; Calciferous Sandstone series, at base of Carboniferous formation.
7. *L.* (*Lepidophloios ?*) *Wunschianum*, Williamson ; also from Lower Carboniferous strata.
8. *L. selaginoides*, Carruthers ; Coal-measures.
9. *L.* (*Lepidophloios*) *fuliginosum*, Williamson ; Coal-measures.
10. *L. intermedium*, Williamson ; Coal-measures.
11. *L. obovatum*, Sternb. ; Coal-measures.

L. mundum, Will., formerly included in this list, has now been shown by Mr. Lomax to be the stem of a *Bothrodendron* (see p. 200).

Now, of all these forms, there are only two which are known to have attained any considerable size without showing secondary growth of the vascular tissues ; these species are *L. Harcourtii*, the first *Lepidodendron* discovered with its structure well preserved, and *L. Hickii*, recently recognised as a distinct species by Mr. D. M. S. Watson. The original specimen of *L. Harcourtii* was found in 1832, in the Hesley Heath Colliery, Northumberland, and was first described by Witham of Lartington,[1] who named it *Harcourtii* after its discoverer. Our first minute knowledge of the structure of this fossil was due to the great French palæobotanist, Adolphe Brongniart, who gave an

[1] *Internal Structure of Fossil Vegetables*, Edinburgh, 1833.

admirable account of the anatomy.[1] Subsequent investigations, especially those of Williamson and Bertrand, aided by the discovery of a few additional specimens, have rendered *Lepidodendron Harcourtii* one of the best known among fossil stems. Mr. Watson regards this species as a *Lepidophloios*. The largest specimen hitherto found has a diameter of over 8 cm. (not counting the leaf-bases), while its stele, or rather the wood, which is alone perfect, is rather more than a centimetre in diameter. The wood forms a broad continuous ring, enclosing a parenchymatous pith (see Fig. 56). The outer edge of the wood is crenulated, having a large number of prominent angles, with furrows between them. It is at the prominent angles that the narrow spiral trachéides are placed; all the interior of the wood is made up of uniform, scalariform elements. Hence it is evident that the whole ring of xylem was centripetally formed, the development having started at the external angles. It appears from M. Bertrand's researches that these angles formed a prominent network on the surface of the woody cylinder; from the lower corners of the meshes the leaf-trace bundles, or rather their xylem-strands, passed out. The attachment of the strands was at the sides of the tracheal prominences, and not at their extreme points. The phloëm, of which the preservation is very imperfect, appears to have formed a narrow continuous band round the wood (see Fig. 56, B).

The leaf-traces passed very gradually outwards through the cortex to the leaves, one bundle entering each leaf. Hence a large number of the outgoing

[1] *Histoire des végétaux fossile*, vol. ii. 1837.

strands are met with in every transverse section of the stem, forming a very characteristic feature (see Fig.

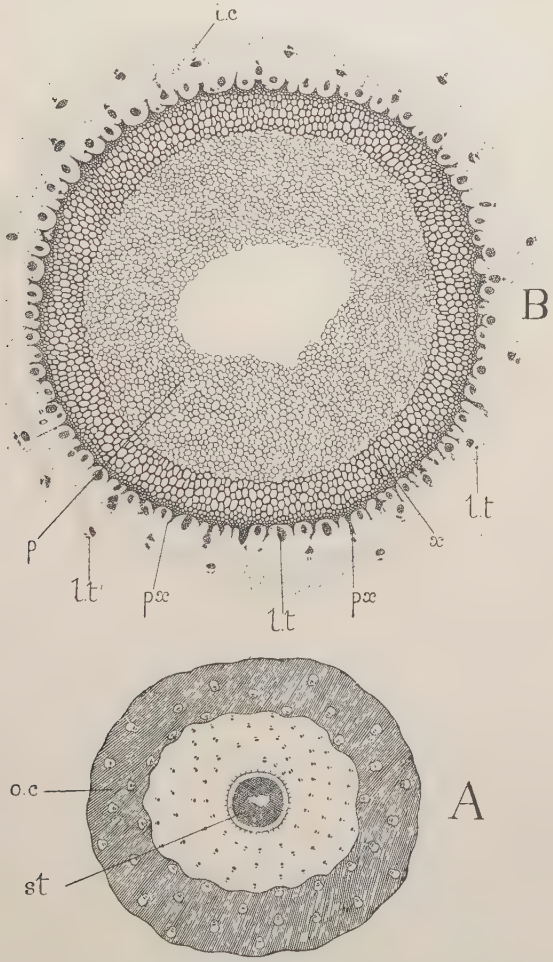

FIG. 56.—*Lepidodendron Harcourtii.* A. Transverse section of stem. *st*, stele; *o.c.*, outer cortex; both here and in the inner cortex the leaf-traces are shown. About nat. size. B. Stele of same. *p*, pith, hollow in middle; *x*, xylem-ring; *px*, protoxylem-points; the leaf-traces join the stele between them. *l.t.*, the leaf-trace bundles, of which the outer, *l.t.'*, show xylem and phloëm; *i.c.*, inner cortex. × 7. Will. Coll. 1594. (G. T. G.).

56, A). They have a complex spiral arrangement, related to that of the leaves to which they ran.[1]

The structure of the individual leaf-trace bundles in *L. Harcourtii* has been described as characteristic of the species; its peculiarity consists in the presence of a conspicuous strand of dark-coloured, apparently fibrous cells, on the outside of the bundle (see Fig. 56, B, *l.t.'*). Other Lepidodendreae, however, show the same structure, as Prof. Seward found in the case of *Lepidophloios fuliginosus*, and Mr. Watson in his new species, *Lepidodendron Hickii*. That the elements in question were really of the nature of hard bast is very improbable. Prof. Bertrand regards them as organs of secretion, comparable to laticiferous cells, and Prof. Seward's observations led him to a similar conclusion,[2] which may be provisionally accepted.

The vascular bundles appear, judging from the best-preserved specimens, to have been of the collateral type, the phloem lying between the xylem and the strand of secretory elements, and perhaps including the latter. The spiral tracheae are placed near the middle of the xylem, a position which they often occupy in the foliar bundles of Lycopods. Outside the phloëm of each bundle, where it traverses the outer cortex, is a large strand of delicate parenchyma, seldom perfectly preserved, which was continuous with the parichnos of the leaf-base.

[1] For a detailed account of the anatomy of *L. Harcourtii*, see Bertrand' *Remarques sur le Lepidodendron Harcourtii de Witham*, Lille, 1891. For *L. Hickii* see Watson. "On a Confusion of two Species under *Lepidodendron Harcourtii*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. li. Part iii. 1907.

[2] A. C. Seward, "Notes on the Binney Collection of Coal-measure Plants," i. *Lepidophloios*, *Proc. Cambridge Phil. Soc.* vol. x. 1899.

The inner zone of cortex consisted of soft parenchyma, usually badly preserved, while the more external region, where the whole tissue was thick-walled, is perfect (Fig. 56, A). The cortex was covered on the exterior by the crowded bases of the leaves, but the latter have often been lost. In the outer cortex, a little below the leaf-bases, periderm was formed at a rather early stage, by the tangential division of the cortical cells. The development of the periderm took place on both sides of the initial layer, and was therefore partly centripetal and partly centrifugal in direction. The leaf-bases were thus separated by a zone of secondary cortex from the inner tissues of the stem, but remained attached to the outer surface of the bark, even on old trunks.

Very definite groups or strands of cells, no doubt of the nature of internal glands, occur in the outer cortex, just within the periderm. These secretory organs are also present in various other Lepidodendreae, as in *Lepidophloios fuliginosus* and in *Lepidodendron Wunschianum*, where they are ranged in concentric bands in the periderm.

Except for the periderm, *Lepidodendron Harcourtii*, as known to us at present, shows no sign of secondary formations. It is, however, perfectly possible that cambial activity may have started at the periphery of the stele, in specimens still larger than any we possess. That this may have been so, is rendered highly probable by the analogy of another species, *L. Wunschianum*, from the Lower Carboniferous strata in the Isle of Arran. In this case secondary wood was formed in great quantity, but it is never found except in stems

of still greater dimensions than the largest known specimens of *L. Harcourtii.*

Williamson sometimes said that it was an unfortunate chance for fossil botany that the first Lepidodendroid stem, of which the structure was investigated, happened to be that of *L. Harcourtii.* The absence of secondary wood in this species, which we now know to have been quite exceptional, led Brongniart to believe that the *Lepidodendra* generally were without exogenous growth. On this ground, he removed *Sigillaria*, in which the secondary tissues were discovered early, both from the Lycopodiaceae and from the Cryptogams, and classed the genus among Gymnospermous Phanerogams. Even when *Lepidodendra* with secondary wood began to be discovered, there was for a long time a strong tendency, on the part of the French school of palæobotanists, to regard all such specimens as really *Sigillariae*, and so to keep up the supposed distinction. We now know, chiefly as the result of Williamson's researches, that most of the Carboniferous *Lepidodendra* agreed essentially with *Sigillaria* in their anatomy, and that the two genera were closely allied members of the Lycopodiales. The controversy, however, proved valuable as a stimulus to research.

Lepidodendron Wunschianum,[1] a species which is abundant in the volcanic beds of Arran, belonging to the oldest part of the Carboniferous formation, essentially resembles *L. Harcourtii* in its primary structure, and needs no detailed description here.[2] Secondary wood has only been found in stems with a primary

[1] Possibly referable to the genus *Lepidophloios.*

[2] Seward and Hill are inclined to identify these two types, but I do not find sufficient evidence to justify us in uniting them.

xylem-cylinder 2 cm. or more in diameter. Cambial growth here went on vigorously, producing a zone of wood nearly 3 cm. thick in the larger trees, some of which were a couple of feet in diameter. In one particular specimen the state of preservation was very remarkable. To quote Williamson's words :—"At Laggan Bay [Arran] the bases of thirteen large stems stood erect and closely aggregated. Further investigation showed that twelve of these were merely cylinders of outer cortex, all their more internal tissues having disappeared and been replaced by volcanic ash, with which the trees had been destroyed and buried. The decay of the softer portions of the bark had loosened all the harder vascular structures compassing their several steles, and allowed them to float out when the area became submerged. But the exceptional stem had met with different treatment. In the first instance, it also had lost all its vegetable contents, which had evidently floated out upon the neighbouring waters. Directed by some fortunate current, a quantity of the floating débris had been washed back into and filled the vacant cavity of the thirteenth stem. Further examination of this débris showed that it consisted of fragments of bark and of Stigmarian rootlets, including a fragment of a vascular axis of a *Stigmaria* ;[1] but what was still more important, we found in it the entire and fully developed steles of no less than five of the remaining trees, which had been tumbled into this single one."[2]

[1] We shall see further on that these *Stigmariae* were the rhizomes or roots of the *Lepidodendra* themselves, and of the allied *Sigillariae*.

[2] Williamson, "Growth and Development of the Carboniferous Arborescent *Lepidodendra*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* ser. iv. vol. ix. p. 45, 1895.

The base of this curious stem, showing all the steles thus accidentally enclosed in it, is now preserved in the Museum of the Owens College, at Manchester.

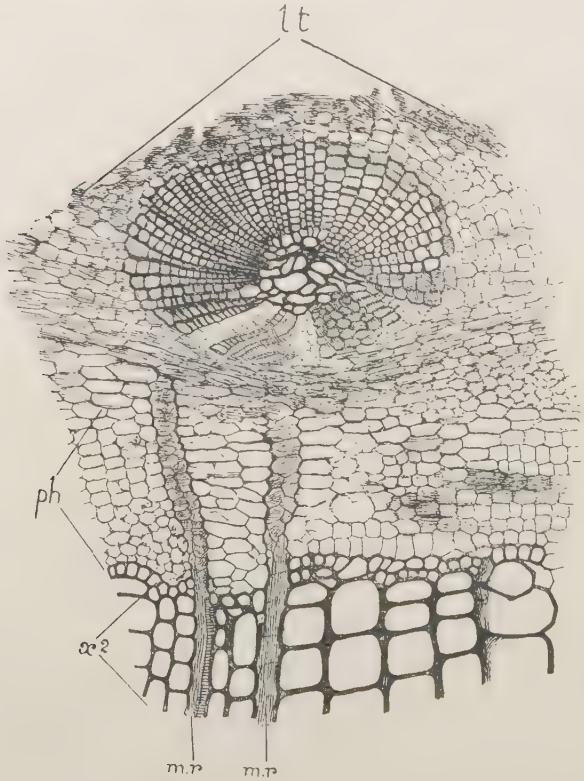

FIG. 57.—*Lepidodendron* (*Lepidophloios*?) *Wunschianum*. Transverse section from outer part of stele, showing leaf-trace. x^2, secondary wood; *m.r*, medullary rays, one of which contains tracheides; *ph*, phloëm (meristematic zone of Seward); *lt*, leaf-trace, with a small mesarch strand of primary xylem, and a broad zone of secondary wood (with short tracheides) and phloëm. × about 55. From a section presented by Mr. Kidston. S. Coll. 1183. (G. T. G.)

A magnificent specimen from Dalmeny (see Fig. 57), referable to the *L. Wunschianum* type, has the interesting peculiarity that the leaf-traces, after leaving

the stele, are accompanied by a broad arc or zone of secondary wood and phloëm, the only case of the kind hitherto found in a Lepidodendroid, as distinguished from a Sigillarian, stem. The specimen is fully described in the *Transactions of the Royal Society of Edinburgh*, by Prof. A. C. Seward and Mr. A. W. Hill.[1]

Another form, which in its primary condition somewhat resembles *Lepidodendron Harcourtii*, is the Burntisland species named by Williamson *L. brevifolium*. This, like *L. Wunschianum*, comes from the Calciferous Sandstones, at the base of the Carboniferous formation. Twigs and branches of all sizes have been found in abundance, and the first beginnings of secondary growth have thus been traced. The species differs strikingly from *L. Wunschianum*, in the dimensions of the branches with secondary tissues. In *L. brevifolium*, even comparatively small twigs have a zone of radially seriated wood of cambial origin, surrounding a primary cylinder, sometimes only about 3 mm. in diameter. In the larger branches, the secondary zone of wood attained a thickness enormously greater than that of the primary ring. An example of this stem, at a fairly advanced stage, is shown, in transverse section, in Fig. 58.

For the more detailed study of the structure and development of the stem in a *Lepidodendron* with secondary growth, we will choose, however, another example, namely *L. selaginoides*, which, from the abundance of specimens and their extraordinarily good preservation, has proved exceptionally favourable for investigation.

In this form, which is abundant in the Lower Coal-measures, the specimens showing structure have been

[1] *l.c.* vol. xxxix. Part iv. 1900.

identified, at least with great probability, with those

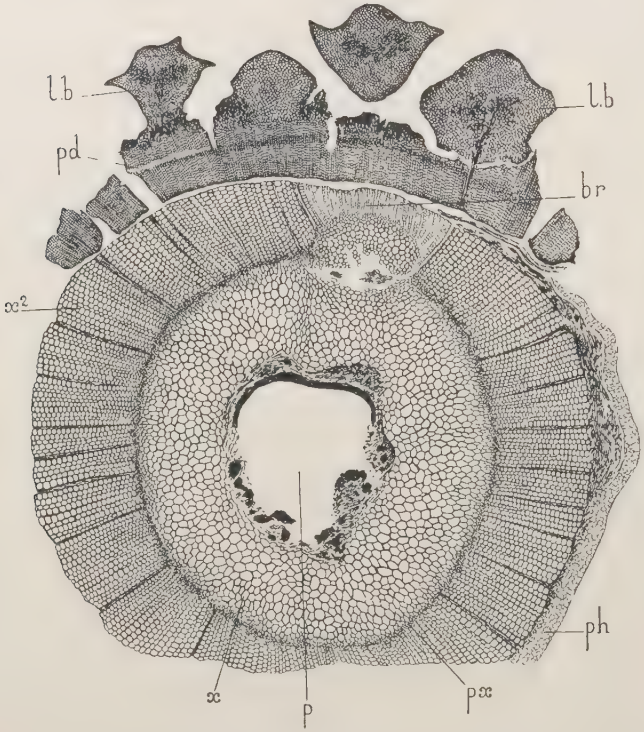

FIG. 58.—*Lepidodendron brevifolium.* Transverse section of stem. *p*, pith, almost wholly destroyed; *x*, broad zone of primary wood; *px*, protoxylem at periphery of primary wood; x^2, secondary wood; *ph*, phloëm; *br*, small stele becoming detached to supply a branch; *pd*, periderm; *l.b*, leaf-bases, showing bundle and parichnos. All the more internal cortex, which once intervened between stele and periderm, has perished. × 4½. S. Coll. 54. (G. T. G.)

preserved as impressions or casts, in which the external characters are visible.[1]

[1] See Carruthers, "Structure of the Stems of the Arborescent Lycopodiaceae of the Coal-measures," *Monthly Microscopical Journal*, vol. ii. 1869. As, however, the identification is not absolutely certain, some authors prefer to use Binney's name, *L. vasculare*, rather than *L. selaginoides*.

Lepidodendron selaginoides is at once distinguished anatomically from the other species by the peculiar structure of the central cylinder. No definite pith is present; the tracheae of the primary wood extend to

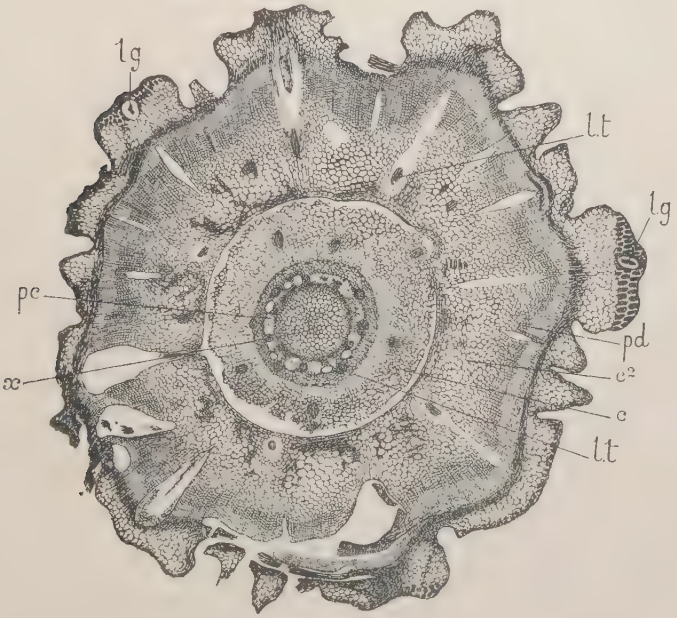

FIG. 59.—*Lepidodendron selaginoides*. Transverse section of young branch, before secondary wood has formed. *x*, primary xylem-cylinder; *pc*, zone of phloëm and pericycle; *c*, inner cortex, differentiated into three layers; c^2, outer cortex; *pd*, periderm; beyond this are the leaf-bases; *lg*, ligule; *l.t*, leaf-traces, at various points on their outward course. × about 7. S. Coll. 1376. (G. T. G.)

the centre of the stele (Figs. 59 and 60). The outer part of the primary xylem has the structure usual in the genus; at the extreme periphery there are a number of slightly prominent points, at and near which the spiral elements are placed. Here then, as in other

forms, the development of the xylem must have been centripetal. Immediately within the protoxylem the elements become much larger, forming a broad continuous zone, which consists exclusively of long scalariform tracheides, without any admixture of parenchyma (Figs.

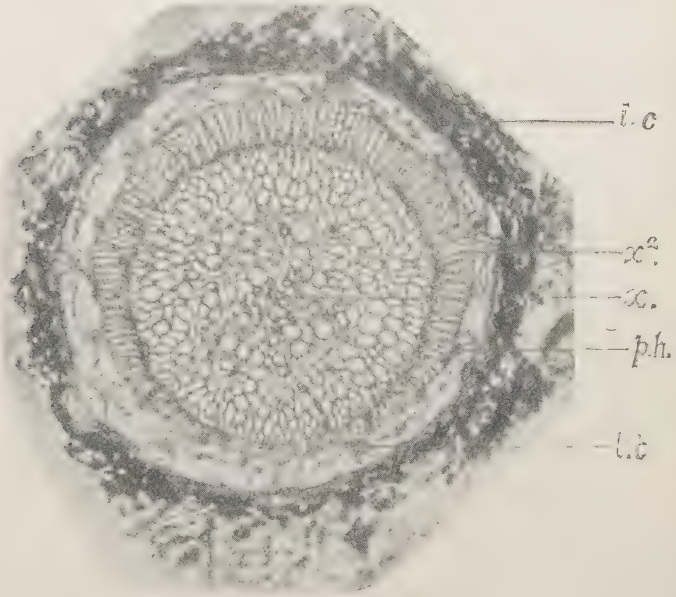

FIG. 60.—*Lepidodendron selaginoides*. Transverse section of stele after commencement of secondary thickening. *x*, primary xylem-cylinder, with reticulate tracheides in central part, and small protoxylem-elements at periphery; x^2, secondary wood, unequally developed; *ph*, phloëm-zone; *i.c*, part of inner cortex; *l.t*, leaf-traces. × 17. From a photograph by Dr. Bousfield. S. Coll. 17.

60 and 61). As we advance further inwards, however, parenchyma begins to make its appearance, and at the same time the tracheides change their character, becoming much shorter, with horizontal transverse walls (Fig. 60, *x*). Thus the whole central part of the stele is occupied by mixed tracheides and parenchyma.

The former are often no longer than the cells which accompany them. The transverse walls of the short tracheides are reticulately thickened, and form a conspicuous feature in the transverse sections, by which the species can be easily recognised.

The phloëm, which is fairly preserved in some of the best specimens, forms a zone of thin-walled tissue, including strands of elongated elements, surrounding the wood, and itself surrounded by a somewhat broader band of larger-celled parenchyma, which may be regarded as the pericycle. The leaf-trace bundles, where they cross this zone, are each enclosed in a special sheath, sometimes forming a kind of bridge or trabecula across the more delicate tissues of the phloëm and pericycle (Fig. 60).

The endodermis is simply a layer of tangentially elongated cells. Then we come to the broad zone of inner cortex, which consists of delicate short-celled parenchyma, only preserved in the best specimens, as in that shown in Fig. 59. The more internal layers, however, are of firmer structure, and often persist when the rest has perished. In the middle part of this zone the cells show some trace of radial arrangement. Through this region the leaf-trace bundles pass, still taking a steep upward course (Fig. 59). Beyond the inner cortex is another broad belt, the outer cortex, the tissue of which is formed of elongated cells with, for the most part, rather thick cell-walls; this zone, owing to its solid construction, is always well preserved. The leaf-traces, which in this region gradually assume a more horizontal course, often pass through gaps, due to the disappearance of delicate tissue (Fig. 59).

The outer cortex ends at the exterior of the stem in the zone of the leaf-bases, which collectively cover almost the whole surface. The tissue immediately within the leaf-bases remained thin-walled, for it was here that the phellogen arose.

The leaf-trace bundles start, so far as their xylem is concerned, directly from the angles of the primary wood, and not between them, as in *L. Harcourtii*. The leaf-traces are normally collateral, with xylem directed inwards and phloëm, consisting of elongated narrow elements, outwards. The spiral elements, where their position can be determined with certainty, lie on the inner edge of the xylem, which was thus, as a rule, *endarch*, another point of difference from *L. Harcourtii*, where the structure in the corresponding region was regularly *mesarch*.[1] The soft bast is bounded on the exterior by some elements with thicker cell-walls, which may be most probably interpreted as secretory sacs. The whole bundle is surrounded by a well-marked sheath.

Where the leaf-trace enters the denser outer cortex, a large strand of delicate parenchyma—much larger than the bundle itself—accompanies the latter on its lower side,[2] and passes out with it into the leaf-base; here the parenchymatous strand forks into two, the two branches diverging to the right and left of the bundle. It is these strands of tissue which give rise

[1] These are convenient terms for shortly characterising the development of the wood of a vascular bundle. If the protoxylem lies on the inner side the strand is *endarch*; if in the middle of the xylem, *mesarch*; if on its outer side, *exarch*.

[2] Indicated by the gaps accompanying the leaf-trace bundles in Fig. 56, A, from *L. Harcourtii*.

to the two lateral prints on the leaf-scar, called the parichnos (cf. Fig. 62). This structure is common to the Lepidodendreae in general.

We have so far considered the anatomy of the stem in its primary condition; in most of the specimens the structure is modified by the appearance of secondary tissues, namely, of periderm in the outer cortex, and of new wood and bast around the stele. In *L. selaginoides* even the smallest twigs found (which, however, are not usually less than 1 cm. in diameter) may show both these new formations, while in some of the other species, as we have seen, the secondary wood and bast appear to have been limited to the main stem and its principal branches.

The periderm began to appear early; in some of the younger specimens its first origin can be traced. It was developed from a zone of cells of the outer cortex, lying immediately within the leaf-bases, between which it was only separated by a few cells from the outer surface of the stem. This zone of tissue became meristematic; its elements divided tangentially, and acted as a phellogen, producing a very large quantity of secondary cortical tissue (see Fig. 59, *pd*, and compare Fig. 58). There has been some difference of opinion as to the position of the phellogen in the older specimens, but there is now little doubt that it lay in the outer part of the secondary zone, so that the larger portion of the new tissue was produced on its inner side, and a smaller portion towards the exterior. Thus the greater part of the secondary cortical zone, as it was produced on the inside of the generative layer, is to be regarded as phelloderm. Whether the smaller outer portion

was really of the nature of cork is doubtful—the more so, as the bases of the leaves outside it certainly persisted for a very long time.

The periderm (as we may call the whole of the secondary cortical tissue) consisted of elongated, rather thick-walled cells, and must have contributed very materially to the mechanical strength of the stem. It may have had other functions as well, and was certainly much more than a mere bark.[1] The late M. Hovelacque, to whom we owe the most detailed study of the anatomy of this species,[2] was mistaken in supposing that the periderm was formed entirely from within; on its inner margin the tissue is, as a rule, thick-walled, and quite unlike a meristem, while a delicate zone of cells is constantly to be found in its outer part (see Fig. 59). It appears probable, however, that additions may sometimes have been made to the periderm from the interior also, new layers of primary cortical cells taking up the divisions.

In old specimens, the periderm attained a thickness of as much as 2 inches. The course of the leaf-trace bundles through it is marked by radial strands of tissue more delicate than the rest. The periderm also shows concentric markings, due to the alternation of zones of wider and narrower elements. What has been said of the periderm of *Lepidodendron selaginoides* may be taken as holding good for the genus as a whole (cf. Figs. 58 and 59).

[1] In *L. Wunschianum* it contained strands of cells probably with a secretory function.

[2] Hovelacque, "Recherches sur le *Lepidodendron selaginoides*," *Mém. Soc. Linnéenne de Normandie*, 1892. This fine memoir is magnificently illustrated.

The secondary vascular tissues began to develop rather later than the periderm. Very often the new growth began on one side of the central cylinder, so that for a time the secondary wood formed a crescent, and not a complete ring (cf. Fig. 60); in other cases it was fairly equal all round from the first. The cambial

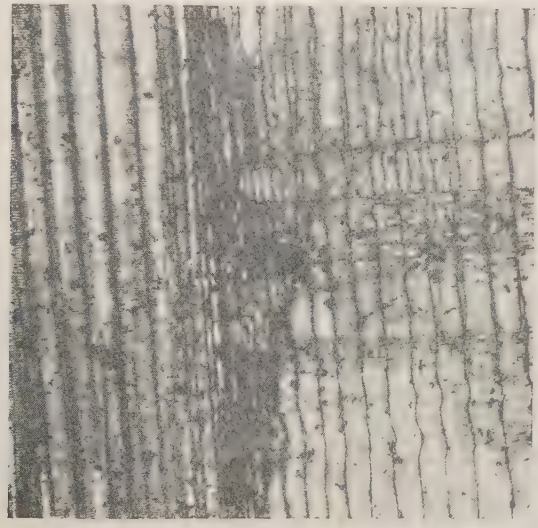

Fig. 61.—*Lepidodendron selaginoides.* Part of radial section, showing primary wood on left, and secondary wood, with medullary rays, on right; the narrow elements between the two are the protoxylem. × about 25. From a photograph by Dr. Bousfield. S. Coll. 24.

divisions started in the conjunctive tissue between the primary wood and phloëm; the very first beginning of the new formation can be traced in some of the specimens (see Fig. 60, on lower side of figure). The secondary wood usually abuts directly on the small external tracheides of the primary ring (see longitudinal section, Fig. 61); sometimes a layer of

parenchyma intervenes. The secondary wood consists of regular radial series of tracheides, with medullary rays between them; the tracheal rows are more numerous than the rays. The secondary tracheides, like the primary, are scalariform (Fig. 61), with the pits on their tangential as well as their radial walls. The rays vary much in height and width; sometimes a ray consists of a single row of cells; sometimes it is one cell thick, but many cells high; while in other cases the middle part of the ray is several cells in thickness. We must remember that these rays are only called "medullary" from analogy with those of other plants; in *Lepidodendron* they do not really reach the pith, even where one is present, because the ring of primary wood is quite continuous, so as to shut off the rays completely at their inner ends. The muriform character of the rays, as seen in radial section, is shown in Fig. 61.

The leaf-traces, or rather their woody portions, extend through the secondary wood, traversing enlarged medullary rays. Quite apart from the leaf-traces, however, the rays generally contain numerous reticulated or spirally thickened elements, which probably served to keep up water-communication in the radial direction throughout the wood; they would thus be analogous to the tracheides occurring in the medullary rays of many of the Coniferae.

The phloëm underwent comparatively little increase, at least during the earlier stages of cambial activity. In the older stems, where the secondary wood reaches a thickness of half an inch, the phloëm is seldom preserved. The actual amount of new vascular tissue

was small compared with the much greater development of periderm.

Although the details of the cambial growth have not yet been satisfactorily cleared up, there is no doubt that it was normal, in the sense that the cambium produced wood internally, and phloëm, though probably to no great extent, on its external side.

The cells of the cambium in Lepidodendreae, where preserved, are not usually found to correspond exactly to the radial series of xylem-elements on their inner side (cf. Fig. 57). It appears probable that the same initial layer was not active throughout the duration of secondary growth, but that new zones of cells may have taken up the cambial divisions periodically. In this respect there would be a certain similarity to the secondary increase in *Isoëtes*, among living plants.

The phloëm of the Lepidodendreae also presents considerable difficulties. Typical phloëm, consisting of delicate elongated elements, has not always been recognised, even in the best-preserved specimens, such as that illustrated in Fig. 57. In other cases, however, as in the leaf-traces of *L. selaginoides* and in the vascular bundles of the cones, the phloëm appears to have been quite of the normal type,[1] so we are not justified in supposing that there was any fundamental difference in this respect between the Lepidodendreae and their recent allies.[2]

[1] See Maslen, "Structure of *Lepidostrobus*," *Trans. Linn. Soc.* vol. v. 1899, Plates xxxvi.-xxxviii. Figs. 11, 13, 14, and 33.

[2] On the controversy as to phloëm in Lepidodendreae, see F. E. Weiss, "On the Phloëm of *Lepidophloios* and *Lepidodendron*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. xlv. Part iii. 1901; and Seward, "The So-called Phloëm of *Lepidodendron*," *New Phytologist*, vol. i. 1902.

Before leaving the subject of the anatomy of the Lepidodendroid stem, it is of some interest to note that in *Lepidophloios fuliginosus* (Williamson), a species which resembles *Lepidodendron Harcourtii* so closely that for many years they were not distinguished, a certain amount of secondary xylem was formed. It was, however, much less regular than in the other species which show it, such as *Lepidodendron selaginoides* or *L. brevifolium*. In *L. fuliginosus* the cambium was an anomalous one, arising irregularly in various parts of the phloem-zone and pericycle. It produced a good deal of secondary parenchyma, among which there are usually scattered groups of wood; the secondary tracheides have a very sinuous and irregular course. In some cases tracheides appear to be altogether absent from the secondary zone. We may regard this species (which, from the form of its leaf-bases, must certainly be referred to *Lepidophloios*, as first pointed out by Cash and Lomax in 1890) as exhibiting either a primitive and rudimentary or a reduced form of secondary growth. In a rather doubtful species, *Lepidodendron intermedium*, there is a similar mode of secondary thickening; this form derives its specific name from combining to some extent the characters of *Lepidophloios fuliginosus* and *Lepidodendron selaginoides*.

Two new cases have recently been described in which the external features of a petrified specimen are preserved, so as to allow of its reference to a definite species, based on the superficial characters, while at the same time the internal structure can be investigated. In a stem clearly referable to *Lepidodendron obovatum*, Sternb., various details of the anatomy, and especially

the presence of a parenchymatous secondary zone, show a close agreement with *Lepidophloios fuliginosus*.[1] Curiously enough, the other specimen in question, referred by Mr. Seward to *Lepidodendron aculeatum*, Sternb., likewise "exhibits an exceedingly close agreement with that type of structure which it has been customary to describe as *Lepidophloios fuliginosus*."[2] It is thus evident that no anatomical distinction can be drawn between the two so-called genera *Lepidodendron* and *Lepidophloios*.

3. *Leaves*.—We next come to the structure of the leaves of the Lepidodendreae. It is, of course, necessary to distinguish between the leaf-bases or cushions, which remained in connection with the stem, and the leaves themselves, which were thrown off. The great majority of the specimens with structure preserved bear the leaf-bases only; in the literature it has sometimes happened that the latter have been confused with the actual leaves.

The external form of the leaf-base has already been described. We have also seen that on the scar, left by the fall of the leaf itself, there are three prints (cf. Fig. 55, p. 130). The middle one is caused by the vascular bundle, which remained simple throughout the leaf. The two lateral prints, called the parichnos, are, as stated above, of quite a different nature; a strand of large-celled parenchyma accompanies the leaf-trace through the outer cortex on its lower side, and divides, in the base of the leaf, into two strands, which take up their position to the right and left of the vascular bundle. When the

[1] Scott, "Structure of *Lepidodendron obovatum*," *Ann. of Bot.* vol. xx. 1906, p. 317

[2] Seward, "Anatomy of *Lepidodendron aculeatum*," *ibid.* p. 378.

leaf fell off, the broken ends of these two parenchymatous strands appeared on the scar, with the print marking the bundle between them (see Fig. 62, showing the leaf-bases of a *Lepidophloios* in tangential section).

The two external prints on the surface of the leaf-

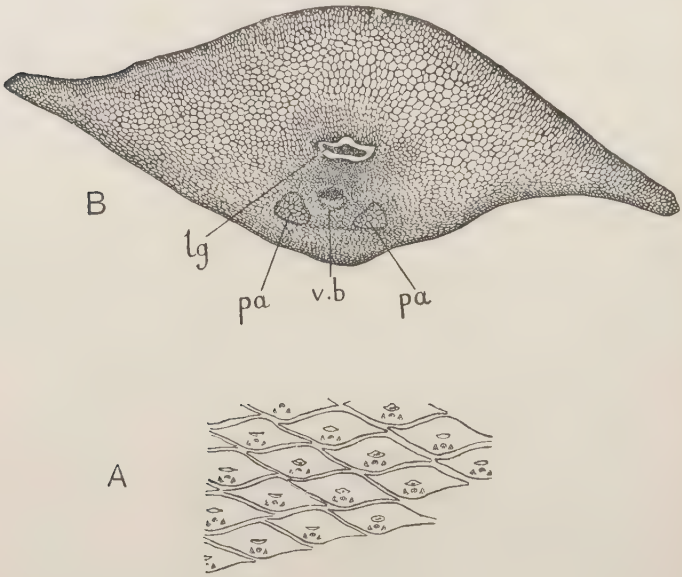

FIG. 62.—*Lepidophloios*, sp. A. Tangential section from the outside of a stem, passing through the leaf-bases, and showing their characteristic form. Slightly enlarged. B. A single leaf-base, to show details. *v.b*, collateral vascular bundle; *pa*, the two parichnos-strands; *lg*, ligule in its pit. × 10. Will. Coll. 1974 A. (G. T. G.)

cushion below the scar (see Fig. 55 *a*, *a*) were in connection with the parichnos, as was first shown by Potonié in a *Lepidophloios*. Professor Weiss has recently investigated the structure, and finds that in *Lepidophloios* the parichnos-strands run very close to the surface and communicate with a delicate sub-epidermal tissue containing well-developed intercellular spaces. In a *Lepidodendron*,

probably *L. Hickii*, Watson, this lacunar tissue lies at the base of the depressions which constitute the external prints. There appear to have been numerous stomata in the overlying epidermis.

The parichnos-strands die out in the leaf itself, losing themselves in the mesophyll. Thus the parichnos-tissue kept up communication between the delicate parenchyma of the inner cortex and the assimilating mesophyll of the leaves, as well as with the patches of aërenchyma in the persistent leaf-bases. The function may probably have been to facilitate respiration.[1] Mr. T. G. Hill has lately shown that strands comparable to the parichnos occur in the leaves of *Isoëtes Hystrix* and various species of *Lycopodium*; in these cases the function of the strands is secretory, as may sometimes have been the case in fossil Lycopods.[2]

The little triangular print on the upper part of the cushion, immediately above the leaf-scar, is of special interest, for we now know that this represents the *ligule*, an organ which is characteristic of *Selaginella* and *Isoëtes*, though absent from the other recent genera of Lycopods. Stur was the first to identify the ligule in *Lepidodendron*, but until it was demonstrated in specimens with structure preserved, there was no proof of the correctness of his interpretation. The presence of a ligule was proved almost simultaneously by Count Solms-Laubach[3] in specimens from the Lower Carboniferous of Silesia, probably referable to the *L. brevifolium*

[1] F. E. Weiss, "The Parichnos in the Lepidodendraceae," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. li. 1907.

[2] T. G. Hill, "On the Presence of a Parichnos in Recent Plants," *Ann. of Bot.* vol. xx. 1906.

[3] *Bot. Zeitung*, 1892, p. 110, Plate ii. Figs. 2 and 4.

of Williamson, and by the late M. Hovelacque[1] in *L. selaginoides*. It has since been demonstrated in several other species, and was probably common to the whole family.

In all the species in which the ligule has been found, it presents much the same features. Its position is always on the upper surface of the cushion, immediately above the leaf-scar.

The ligule is seated at the base of a deep flask-shaped cavity, and is very rarely found projecting beyond it (see Figs. 62, B, and 63, *lg*). The ligule was, of course, a delicate organ, and is often imperfectly preserved; often the ligular cavity is shown, when the ligule itself has perished altogether. In some cases, however, the cellular structure of the ligule is perfectly shown, and is found to agree, on the whole, with that in recent Ligulatae. The deep ligular cavity is very characteristic of Lepidodendreae, but is not without parallel among recent plants, for Professor Harvey Gibson has shown that in *Selaginella oregana* and *rupestris* "the free margin of the ligule scarcely appears above the edge of the very deep pit in the leaf in which it is seated."[2]

The base of the ligular cavity lies just above the vascular bundle, and is in many cases, if not in all, surrounded by a sheath of short tracheides, forming a connection with the wood of the leaf-trace bundle, just as in *Isoëtes* and in some *Selaginellae* among recent plants. The cavity slopes from its base, upwards and

[1] "Recherches sur le *Lepidodendron selaginoides*," *Mem. de la Soc. Linnéenne de Normandie*, Caen, 1892.

[2] "Anatomy of the Genus *Selaginella*," Part ii. The Ligule, *Annals of Botany*, vol. x. p. 83, Plate viii. Fig. 19, 1896.

outwards, opening just above the scar, where the leaf itself was inserted (see Fig. 63). The print on the casts corresponds to the mouth of the ligular cavity.

The presence of a ligule in Lepidodendreae is an interesting discovery, indicating affinity with *Selaginella* or *Isoëtes*, rather than with *Lycopodium*, among recent members of the order. There are a few other facts which point in the same direction, but it is not likely

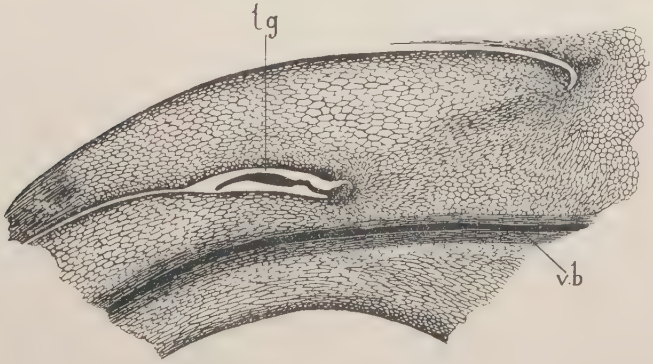

FIG. 63.—*Lepidophloios*, sp. Radial section of a leaf-base from the same specimen as Fig. 62. *v.b.*, vascular bundle of leaf; *lg*, ligule, seated in a deep pit, communicating by a canal with the upper surface. × 10. Will. Coll. 1960. (G. T. G.)

that the relation to any recent genus was at all a close one.

The structure of the free part of the leaf was thoroughly worked out by M. Renault [1] in a species (*L. esnostense*) from the Lower Carboniferous rocks (Culm) of France; certain leaves, associated with, and probably belonging to the British form *L. Hickii*, Watson, agree in several respects with the French specimens, while leaves of other British Lepidodendreae are also similar. In

[1] *Flore fossile d'Autun et d'Epinac*, Part ii. p. 178, Plate xxxiv. Figs. 4-8.

L. esnostense the leaves were acicular, and not very different in form from those of some species of *Pinus*. Along the under surface, on either side of the midrib, are two furrows, which are very deep near the base

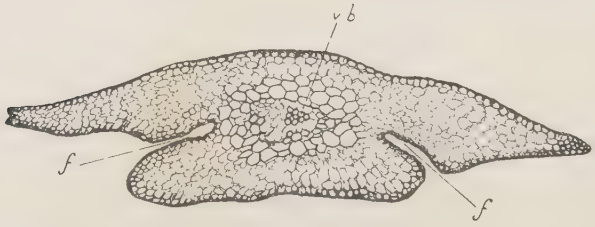

FIG. 64.—*Lepidodendron Hickii*. Transverse section of leaf *v.b.*, vascular bundle; some of the large elements round it constitute the transfusion-tissue; *f*, furrows in which the stomata are placed. × 60. S. Coll. 51. (G. T. G.)

of the lamina, but become less marked towards the apex. It is on the epidermis lining these furrows that the stomata are found. They are very numerous, and of the usual bicellular structure. The rest of the leaf is covered by a small-celled epidermis with a

FIG. 65.—*Lepidodendron Hickii*. Epidermis of leaf, with stomata. × about 300. S. Coll. 51. (G. T. G.)

thick-walled hypoderma below it. The mesophyll consists of a spongy tissue, like that of many recent leaves. This was no doubt the green, assimilating part of the leaf when alive. The middle of the leaf is traversed by a central strand of tissue, enclosing the vascular bundle. The bundle itself is small, but it is surrounded by a wide zone of spiral or reticulated

tracheae, much larger and more numerous than those of the xylem itself. This peculiar formation appears to have been analogous to the transfusion-tissue in the leaves of Coniferae. In the leaf of *Lepidodendron*, as in that of the Coniferae, there is some ordinary parenchyma surrounding the bundle, in addition to the tracheae.

In the leaves referred to *L. Hickii*, the structure is much like that just described, except that their form was not acicular, but linear, or narrowly lanceolate, the leaf having a lamina of some width (see Fig. 64). The stomata are extremely well shown (see Fig. 65), and appear to have occupied the same position as in the French species.

In the structure of the leaves, as in so many other points, we see that the Palæozoic Lycopods were more highly organised than their representatives in our own period.

4. *Branching.*—We now come to the question of the branching of the stem. So far as the external and anatomical characters enable us to judge, the branching was dichotomous throughout, and it is usual to assume that this was the case, though, in the absence of any knowledge of the growing point, it is impossible to say whether the strict definition of dichotomy applied here.

We must distinguish, with Williamson, between equal and unequal dichotomy. The former prevailed in the forking of the main stem and its principal branches, where the two limbs into which the parent axis divided were similar (Fig. 66). Immediately below the dichotomy the stele separates into two

parts, which for some distance have the form of horse-shoes, with the pith of each stele open towards the other. Where there was secondary growth, the cambium in this

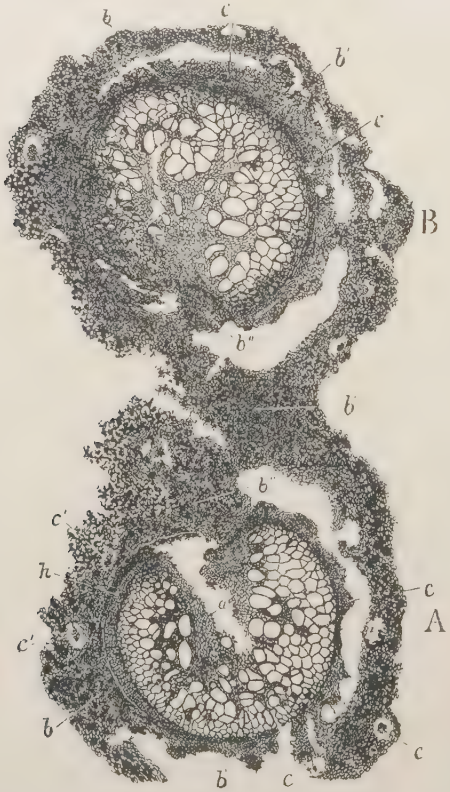

FIG. 66.—*Lepidodendron selaginoides.* Transverse section showing the two steles (A and B) of a bifurcating stem. *a*, pith; *b*, inner cortex; *c*, leaf-traces; *h*, secondary wood. The pith in this species only exists near a bifurcation, where the steles are still incomplete on the inner side. × about 9. After Williamson, *Phil. Trans.* Will. Coll. 340.

region sometimes extended into the medulla, forming an inverted band of secondary tissues within the primary wood. This occurred even in *L. selaginoides*, where the

pith was replaced by scattered parenchyma. Although limited to the place of bifurcation, this condition is of some interest, because analogous anomalies occur among the higher plants at the present day. The cambium, in fact, shows similar eccentricities in its behaviour wherever it occurs, quite irrespective of taxonomic relationship. As we trace the two branches higher up, we find that the stele in each gradually regains its normal circular form. (Fig. 66, from a forking branch of *L. selaginoides*, shows the steles in an intermediate state.)

Unequal dichotomy simply means that one branch of the fork is much smaller than, and sometimes differently organised from, the other. This no doubt often occurred in the vegetative region, in cases where a main axis bore a comparatively small twig, as an apparently lateral branch. Unequal dichotomy was, however, of common occurrence in connection with the fructification, when one branch of a dichotomy was fertile, while the other remained vegetative. Such cases, however, will be considered in the next chapter.

Anatomically, unequal dichotomy is characterised by the behaviour of the stele. It is frequently the case that the smaller of the two branches has no medulla. Then, instead of the two equal horse-shoes described above, we find only a small part of the main stele diverging to the minor branch. Sometimes a segment of the wood was cut out, as it were, from the stele, leaving a small opening, which soon closed up. The segment destined for the branch was thus solid from the first (*e.g. Lepidophloios fuliginosus*, Fig. 69, *b'*). In other cases the strand of wood passing out to the smaller

member was so insignificant that the continuity of the main ring was never interrupted, a group of its more external tracheae sufficing to supply the wood for the branch (see Fig. 58, *br*, from *L. brevifolium*).

To complete the description of the vegetative organs of the Lepidodendreae, we ought now to describe the root. As, however, we cannot as yet distinguish with certainty between the underground organs of *Lepidodendron* and those of *Sigillaria*, it will be necessary to postpone their consideration until the latter genus has also been described.[1]

[1] The anatomy of Lepidodendroid stems was dealt with by Williamson in Parts ii., iii., ix., x., xi., xii., xvi., and xix. of his series of memoirs in the *Philosophical Transactions*, 1872-93. Some of his final conclusions are summed up in his last work, "Growth and Development of the Carboniferous Arborescent *Lepidodendra*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* ser. iv. vol. ix. 1895.

CHAPTER VI

LYCOPODIALES—*continued*

Ulodendron and Halonia; Fructifications of Lepidodendreae; Bothrodendron

1. *Ulodendron and Halonia.*—In the last chapter we described the morphology of the stem and leaf of the Lepidodendreae; we have now to consider their organs of reproduction. Before going on to the cones, something must be said as to two forms of Lepidodendroid stem (commonly regarded as bearing the fructifications) which differ so conspicuously from the ordinary type that they were long described as belonging to distinct genera, to which the names *Ulodendron* and *Halonia* were given. The genus *Ulodendron* is still kept up for certain species by M. Zeiller.

The Ulodendroid form of stem is often of large size, attaining in some cases a diameter of about a foot, and is sometimes dichotomously branched. The general surface bears the ordinary markings of the Lepidodendreae; where the leaf-bases are perfect they present, however, in some cases, according to Mr. Kidston, the characters of a *Sigillaria*, and so do not come under our immediate subject, but in other specimens the superficial characters are clearly those of a *Lepidodendron* (see

Fig. 67). The characteristic feature of the *Ulodendron* stem consists in the presence of roundish scars, often of very large size, usually arranged alternately in two vertical rows, one row on each side of the stem. On the larger *Ulodendra* these scars have a diameter of from 4 to 6 inches. Within the scar, usually somewhat below the centre, is a print or stump, representing either the stalk or the woody cylinder of some lateral appendage. The scar as a whole is depressed, having the form of a shallow cup, with the print or *umbilicus* at the bottom (see Fig. 67). The surface of the cup is usually marked with radiating ridges on the part above the umbilicus, while the lower part bears spirally arranged prominent points.

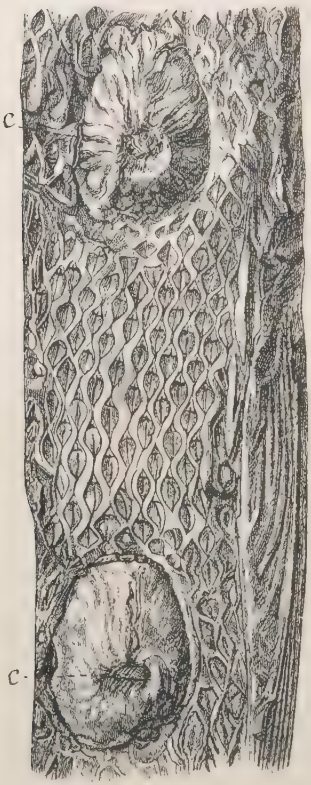

Fig. 67. — *Ulodendron.* Surface of branch, showing two large scars, with the central print *c*, and numerous Lepidodendroid leaf-bases. On the right the leaves are seen. Reduced. After Schimper. The large scars are really depressions, but, owing to the shading, appear in the figure as elevations. They can be seen as depressions if the figure is reversed.

The nature of these curious objects was long in dispute, and is still by no means cleared up, though specimens have been described with "cones" still attached to the scars,[1] thus

[1] D'Arcy Thompson, "Notes on *Ulodendron* and *Halonia*," *Trans.*

appearing to confirm by direct evidence an idea which had long previously been suggested. The *Ulodendra*, then, were supposed to represent the fertile branches of various species of *Lepidodendron* (*e.g. L. Veltheimianum*), *Bothrodendron*, and perhaps *Sigillaria* also, which thus bore their fructifications on thick stems, and not on terminal twigs. The peduncle, represented by the print within the scar, was assumed to be quite short, so that the base of the almost sessile strobilus was in contact with the leafy surface of the main axis; the large cup-shaped scar appeared to have owed its origin to the mutual pressure between the two organs. The great size of the scars in some cases was still, however, unaccounted for, their shape being inconsistent with dilatation by secondary growth.

Mr. D. M. S. Watson [1] has quite recently pointed out the great difficulties involved in the current interpretation of the Ulodendroid scar, and the inadequacy of the evidence in its support. He maintains that the scars are those of caducous branches, which were attached to the whole area of the scar, the umbilicus corresponding to the central cylinder and the dots and radial marks on the scar representing the leaf-traces of the branch. For certain cases, at all events, his interpretation appears to correspond best with the observed facts, though various difficulties remain.

The other form of stem to be considered—that

Edinburgh Geol. Soc. vol. iii. 1880. Cf. Solms-Laubach, *Fossil Botany*, English edition, p. 208. Kidston, "On the Relationship of *Ulodendron* to *Lepidodendron*, etc.," *Ann. and Mag. Nat. Hist.* vol. xvi. 1885; Zeiller, "Sur les *Ulodendron* et *Bothrodendron*," *Bull. Soc. Géol. de France*, sér. iii. t. xiv. 1885.

[1] "On the Ulodendroid Scar," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. lii. Part i. 1908.

known as *Halonia*—has certain points in common with the Ulodendroid branches, but presents a different appearance. The Halonial branch, which, though on the whole smaller than *Ulodendron*, is often several inches in diameter, is characterised by bearing a number of prominent knobs or tubercles, most often spirally arranged (see Fig. 68, A). The general surface is usually badly preserved, the specimens having evidently been partially decorticated before fossilisation. Where, however, the external characters are well exhibited, so as to show the leaf-bases clearly, they prove that the specimens belonged to *Lepidophloios*, though it is quite possible that the Halonial condition may have also occurred in the true *Lepidodendra*. Halonial branches have been found in connection with the ordinary vegetative stems of Lepidodendreae, though whether of *Lepidodendron* or of *Lepidophloios* could not in all cases be determined—a point, however, which is of secondary importance. The fact that the *Haloniae* occurred as ultimate branches of the dichotomous stem,[1] quite disposes of the idea, once maintained by some French writers, that they were of the nature of roots or rhizomes.

As regards the anatomy, the main Halonial axis may either have in all respects the structure of an ordinary vegetative stem, or may differ from it in the absence of a medulla. The latter was the case in a Halonial branch of the Arran species, *Lepidodendron Wunschianum*, investigated by Williamson.[2] The

[1] See Williamson, "Organisation, etc.," Part xii., Plates iii., iv., 1883.

[2] "Organisation, etc.," Part xii. 1883. This species was perhaps a *Lepidophloios*.

branch is not quite an inch thick, and contains a stele about 3.5 mm. in diameter. The wood is perfectly solid, consisting entirely of tracheae, without

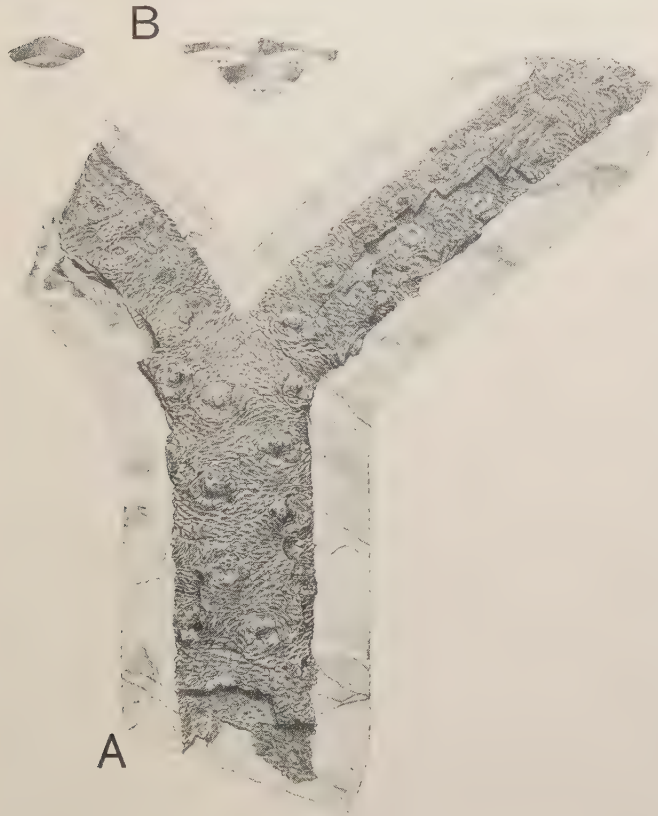

FIG. 68.—*Lepidophloios scoticus*, Kidston. A. Bifurcating Halonial branch, showing numerous tubercles, and the characteristic leaf-bases. About ½ nat. size. B. Leaf-cushions enlarged, showing the scar with the usual three prints. From the Calciferous Sandstone series. After Kidston.

any indication of a medulla. This is not, however, a peculiarity of the Halonial form of branch, for in this species, *L. Wunschianum*, the ordinary vegetative

branches of the same size also have a solid woody axis, and it is only in the larger stems that a pith is present. As regards the leaf-traces and cortical structures, the *Halonia* shows no peculiarities; a thick layer of periderm forms its outer boundary. From the central cylinder small cylindrical steles are given off, which pass obliquely outwards to supply the tubercles (see Fig. 69, *b'*, from *Lepidophloios fuliginosus*). The tubercular steles are surrounded by their own leaf-traces, which no doubt supplied the leaves, borne on the lateral appendages of which the tubercles are the persistent bases.

In *Lepidodendron Hickii* similar tubercles have been observed on some of the smaller branches. In this case the branch itself has the ordinary structure of the species, with a medullate stele, while the small strands running out to the tubercles are without any pith. A similar condition has been found in *Lepidodendron obovatum* and in *Lepidophloios fuliginosus* (Fig. 69). All these cases afford striking examples of the so-called unequal dichotomy described in the last chapter (p. 163).

What then was the nature of these Halonial branches, which evidently did not constitute a separate genus, but occurred as terminal ramifications on certain Lepidodendroid stems? Their position and structure alike prove that they were neither roots nor root-bearing rhizomes. Evidently they bore some kind of lateral appendages of the nature of branches, but different from the ordinary vegetative twigs.

The distinction between *Halonia* and *Ulodendron* is

not always an obvious one. As a rule the appendages of *Ulodendron* were distichously arranged, while those of *Halonia* were multiseriate, and quincuncially disposed. Williamson, however, described a specimen with

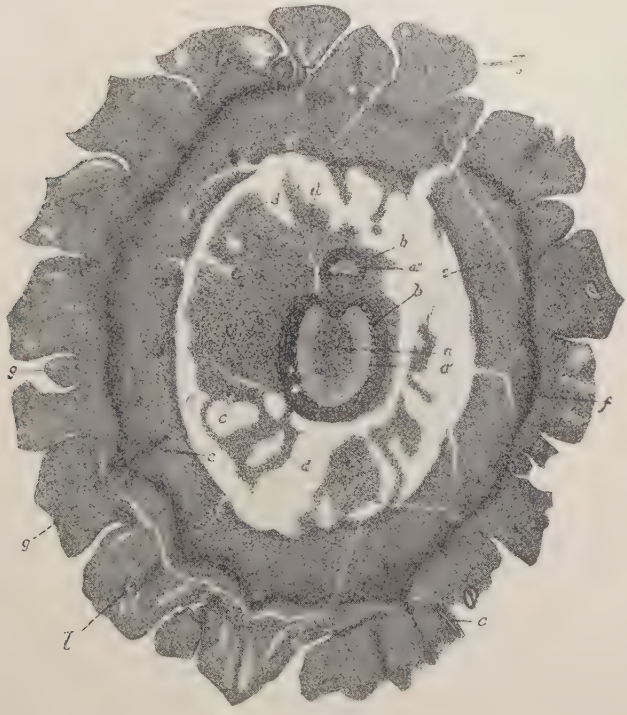

FIG. 69.—*Lepidophloios fuliginosus*. Transverse section of a young shoot (probably in the Halonial condition); *a*, pith, *a'*, xylem, of main stele; *a''*, xylem of branch; *b*, *b'*, phloëm of main and branch steles; *c*, leaf-traces; *d*, inner cortex; *e*, middle cortex; *f*, periderm; *g*, leaf-bases; *l*, ligule. × about 2. After Williamson, *Phil. Trans.* Will. Coll. 379.

multiseriate, quincuncially arranged scars apparently of the *Ulodendron* character, and also a *Halonia* with the tubercles in two series, so this distinction loses its value.[1]

[1] Williamson, xix. Plate vi. Figs. 22 and 25, A.

A magnificent specimen of the latter kind was discovered some years back by Mr. J. Lomax, and described by Prof. F. E. Weiss. The stem, which has a mean diameter of about 8 cm., bears, on opposite sides, two series of large tubercles, with all the characteristics of *Halonia*. The main stem, the structure of which is perfectly preserved, agrees very closely with that of *Lepidophloios fuliginosus*.[1] Fig. 69 is from the latter species, and shows a younger branch, also with the Halonial mode of branching and apparently biseriate. These specimens, together with others, in which the leaf-bases are preserved, have been regarded as showing that the Halonial shoots of *Lepidophloios* in some cases bore their tubercles in two rows, though this conclusion is disputed by Mr. Kidston,[2] who considers the attribution of these specimens to *Lepidophloios* as unproved.

The tubercles of *Halonia* appear in most specimens more prominent than they were in nature, owing to the axis which bears them having lost its outer cortex. In specimens with the natural surface preserved, the tubercles appear rather as scars, but are quite distinct from those of *Ulodendron*, owing to the absence in *Halonia* of the cup-shaped area characteristic of the former. The conclusion to which the facts appear to point is that the so-called *Halonia* consisted of fertile branches of *Lepidophloios* (and possibly other Lepidodendreae) bearing deciduous stalked cones.

A specimen figured by Grand'Eury[3] appears to

[1] F. E. Weiss, "A Biseriate Halonial Branch of *Lepidophloios fuliginosus*," *Trans. Linn. Soc. Bot.* ser. ii. vol. vi. 1903.

[2] Kidston, "On the Internal Structure of *Sigillaria elegans*," *Trans. Roy. Soc. Edinburgh*, vol. xli. Part iii. 1905.

[3] Grand'Eury, *Bassin houiller du Gard*, Plate vi. Fig. 17, 1890.

strongly support this conclusion. He represents a portion of a thick stem of *Lepidophloios laricinus*, bearing four slender branches, on which are scales differing entirely from the vegetative leaves. These branches he regards, with great probability, as the peduncles of cones. The specimen seems to be of the same nature as the Halonial branches which are known to occur in this species. It is fair, however, to mention that Grand'Eury, in the same work, still inclined to regard *Halonia* as a rhizome.

From the whole of the facts, we may take it as very probable, though more direct evidence is much needed, that *Halonia* consists of the cone-bearing branches of certain Lepidodendroid plants (especially *Lepidophloios*), the tubercles representing the places where the cones themselves were inserted. In these forms, then, the cones would have been borne on relatively thick branches, but this was not always the case in Lepidodendreae, for there is no doubt that in many species the cones occurred at the ends of slender twigs, the ultimate ramifications of a much-branched stem (see Fig. 53, B, p. 129). Considering the serious doubts that now exist as to the nature of *Ulodendron*, it must be admitted that the question of *Halonia* also demands re-investigation.

2. *Lepidostrobus*.—We now come to the consideration of the actual fructifications. In a few instances, the strobili have been found in connection with the branches of *Lepidodendron*, as, for example, was the case in *L. Ophiurus* (see Fig. 53, B). As a rule the specimens are isolated, but their nature has been determined

by comparison with the cones still in position. In cases where the structure is preserved, additional and convincing evidence is afforded by the anatomy of the axis of the cone, which is quite similar to that of a young vegetative twig of *Lepidodendron.*

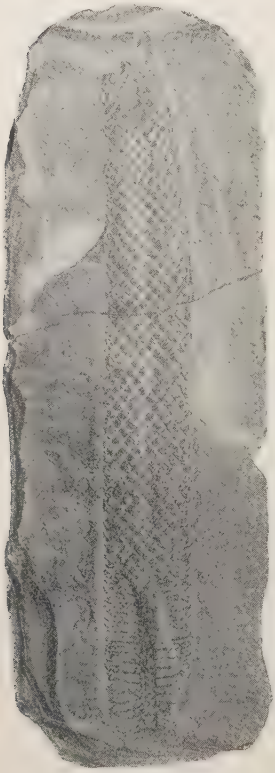

FIG. 70. — *Lepidostrobus Hibbertianus*, Binney. Compressed specimen of an almost perfect cone, with the matrix. The exterior surface is shown, except at the base, where the axis, with some of the megasporangia, is exposed. ⅔ nat. size. After Binney.

As it is very rarely possible to refer the fructifications to the particular species of stem to which they belonged, it is convenient to retain a distinct generic name for them. Most Lepidodendroid cones are described under the name of *Lepidostrobus*, but, as we shall see below, all the fructifications of the group cannot be included under a single genus. For the present we will confine ourselves to the characters of the true *Lepidostrobi.*

The cones of different species vary greatly in their dimensions, the length ranging approximately from about an inch to about a foot. The form is usually cylindrical (Fig. 70), but in some of the shorter cones is more ovoid. The strobilus was either sessile or stalked; the former was no doubt the case if the fruiting stem was ever of the Ulodendroid form, while the

stalked cones were borne either on Halonial branches or on the twigs of the young growth.

The general characters of the cones of *Lepidostrobus* are those of Lycopodiaceous fructifications. In habit the agreement is closest with *Lycopodium*, while in some important details there is a nearer approach to *Selaginella*, but of course the Lepidodendreae have no near affinity with any of the modern genera. The axis of the strobilus bore a very large number of crowded sporophylls (or bracts, as they are often called), usually arranged spirally, but occasionally verticillate. Each sporophyll bore a single sporangium on its upper surface. The sporangia were of large size, enormously exceeding the dimensions of those in existing Lycopods. Thus, in the magnificent specimen known as *Lepidostrobus Brownii*, Schimper, the radial length of the sporangia approaches 2 cm., with a maximum breadth of about 5 mm. The great radial elongation of the sporangia is characteristic of the genus, and is correlated with the peculiar form of the sporophylls, which consist of a long, slender stalk or pedicel, usually more or less horizontal, terminating in a large lamina, which turns vertically upwards, several sporophylls overlapping each other. There is also usually a shorter downward prolongation of the lamina, so that the form of the whole is somewhat peltate (see diagram, Fig. 71). The sporangium is attached all along its lower side to the upper surface of the horizontal pedicel, but is free from the lamina. In its form, and mode of attachment to the sporophyll, the sporangium resembles that of *Isoëtes*.

The cones are often preserved as casts or impres-

sions; where the external surface is perfect, it is completely invested by the overlapping laminae of the sporophylls, which are closely packed together (Fig. 70). When the preservation is less complete, the free tips of the laminae have perished, leaving only their more solid basal portions, which often assume a hexagonal form from mutual pressure. The fractures of the casts often show something of the internal organisation, the tissues being preserved to some extent, though in a carbonised condition (Fig. 70). It is only, however, in the petrified specimens that the structure is completely revealed.

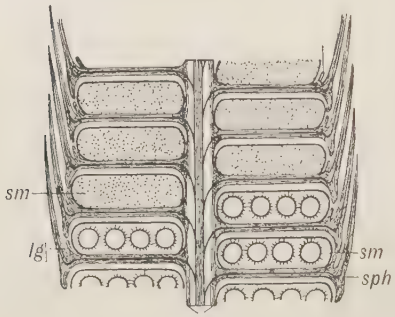

FIG. 71.—*Lepidostrobus*. Diagram of heterosporous cone in radial section. *ax*, axis; *sph*, sporophylls; *sm*, sporangia, seated singly on the upper surface of each sporophyll; *lg*, ligules; the microsporangia, in upper part of cone, contain numerous microspores, while the megasporangia below are shown containing four megaspores each. (G. T. G.)

Our more detailed description will be based on a form named by Williamson *Lepidostrobus oldhamius*,[1] of which several examples in a calcified state have been yielded by the calcareous nodules of the English Coal-measures.

The largest specimens of this strobilus reach a diameter of about 4 cm.; the axis is slender, about 4 or 5 mm. in thickness. The anatomical structure is of the usual Lepidodendroid type. The centre of

[1] For a full illustrated account of the organisation of these cones, see Maslen, "Structure of *Lepidostrobus*," *Trans. Linn. Soc.* vol. v. 1899.

the axis is occupied by a small stele, in which a ring of primary wood surrounds the pith. In the wood the larger elements, which have a scalariform thickening, are towards the interior; the outer margin is produced into a number of somewhat prominent points, and here the narrow spiral elements of the protoxylem are found; thus the development of the wood was evidently centripetal, as in the vegetative stem. In exceptionally well-preserved specimens, the phloëm-zone, surrounding the wood, is preserved; this zone is largely parenchymatous, the elongated elements, presumably forming the true phloëm, occupying only a small space. From some of the best-preserved specimens, it appears that the tissue next the wood was entirely parenchymatous, while the true phloëm lay more to the exterior. In *Lepidostrobus Brownii*, the structure of which is better preserved than that of *L. oldhamius*, a distinct endodermis, separating the stele from the inner cortex, can be traced.

The inner and outer zones of the cortex are usually well preserved in *L. oldhamius*, while the intermediate region has perished—a common condition in the stems of fossil Lycopods. The inner cortex consists of a narrow zone of parenchymatous tissue; beyond this is the gap representing the position of the wide middle cortex; the outer cortical zone is usually perfect, and consists of thick-celled tissue, largely made up of fibrous elements. This zone is continuous on the exterior with the bases of the sporophylls.

The leaf-trace strands, one of which runs out to each sporophyll, have a very steep course, so that a large number, corresponding to several circuits of the

foliar spiral, are seen in transverse section. The structure of these bundles, which is sometimes admirably preserved, is normally collateral. The smallest spiral tracheae lie at about the middle of the xylem-strand, as in *Lepidodendron Harcourtii*. The xylem is surrounded by a layer of delicate parenchyma, which on the outer side separates it from the phloëm. After passing through the inner cortex, the whole bundle is further surrounded by a parenchymatous sheath, continuous with the inner cortical tissue. In this condition it passes through the middle zone of the cortex, where the leaf-trace bundles, with their sheaths, are usually the only tissues preserved.

In *Lepidostrobus Brownii*, where the middle cortex is partly preserved, the leaf-trace bundles are connected with the surrounding tissues by trabeculae, analogous to those radiating from the steles in *Selaginella*. The leaf-traces of *Lepidostrobus* closely resemble those of living Lycopods in structure.[1]

On reaching the outer cortex, where the bundles gradually assume a more horizontal course, the same structure is preserved. Here the sheath, immediately surrounding the vascular strand, has less thick walls than the enveloping cortical tissue. In this region a gap in the tissue constantly appears below each bundle, and accompanies it outwards into the sporophyll. There can be no doubt that this gap was in nature occupied by a delicate parenchyma (sometimes preserved in other species), continuous with that of the middle cortex, and that this tissue, accompanying the leaf-trace,

[1] See Bower, "On the Structure of the Axis of *Lepidostrobus Brownii*," *Annals of Botany*, vol. vii. 1893.

corresponds to the parichnos-strand in the vegetative axis (see pp. 148 and 155).

The sporophylls in *L. oldhamius* are more than a centimetre in length, and stand out at almost a right angle with the axis. Each consists of a long, slender pedicel, terminating in a foliaceous lamina. Near the axis the pedicel is narrow, with a triangular section, while further to the exterior it becomes broader and flatter. It consists chiefly of thick-walled tissue like that of the outer cortex, and is traversed by the vascular bundle, which retains essentially the same structure as in the cortex. The lamina broadens out rapidly at the end of the pedicel, where at the same time it attains a considerable thickness. It turns upwards almost at a right angle with the pedicel, and becomes both narrower and thinner towards its termination. The general form of the lamina is thus lanceolate; as mentioned above, it has a shorter downward prolongation, rendering the whole somewhat peltate (see diagram, Fig. 71). The structure is simple, the mesophyll consisting of rather small-celled parenchyma, in the outer layers of which the cell-walls are much thickened. The single vascular bundle which traverses the lamina is surrounded by a very well developed transfusion-tissue of short spiral or reticulated tracheides, most abundant where the leaf is thickest. In this respect the sporophyll resembles the foliage-leaf, and in both cases this accessory system of tracheides no doubt served to facilitate the supply of water to the mesophyll.

An interesting feature of the sporophyll is the ligule, the presence of which was demonstrated by

Mr. Maslen in *L. oldhamius*. The ligule is seated on the upper surface of the sporophyll, near its distal end, and just where the lamina begins to bend upwards. It is a small pointed body, about half a millimetre in height, with a triangular transverse section, and consists of very small-celled parenchyma. In itself it thus resembles the ligule of the vegetative leaves, but differs in the entire absence of any ligular chamber. In allied forms of strobilus, however, a deep ligular chamber is present. As the discoverer points out, "the position of the ligule in *Lepidostrobus*, with the sporangium between it and the axis, is identical with that in *Selaginella*; but whereas in the latter genus it is quite close to the axis of the cone, in the former the great elongation of the sporangium, which had taken place in the radial direction, had of course carried the ligule with it, and so the latter comes to be situated near the periphery of the cone, and at a considerable distance from the axis. The whole of the horizontal (sporangium-bearing) portion of the sporophyll thus appears to be homologous with the short leaf-base or cushion on the vegetative stem"[1] (see diagram, Fig. 71, *lg*).

The large, elongated sporangium is seated on the upper surface of the pedicel, to which it is attached throughout almost its whole length, from a point close to the axis, up to the beginning of the lamina (see diagram, Fig. 71). The connection between sporangium and sporophyll thus extends for a long distance in the radial direction, amounting to about a centimetre in large specimens of *L. oldhamius*, but at the same time

[1] Maslen, *Annals of Botany*, vol. xii. 1898, p. 259.

the attachment is extremely narrow tangentially, so that a radial section of the cone seldom follows the plane of insertion for more than a small part of its length. Hence the connection between the two organs has sometimes been represented as much less extensive than is actually the case. The pedicel is grooved along its upper surface, and into this groove the narrow band of tissue fits, by which the sporangium and sporophyll are connected. The large baggy sporangium projects on either side considerably beyond the limits of the pedicel.

The wall of the sporangium, as preserved, consists of a single layer of prismatic palisade-like cells, very characteristic of *Lepidostrobus* sporangia, though in some species the wall has a more complicated structure. Along the lower side of the sporangium, where it is attached to the sporophyll, a pad of delicate tissue rises into its cavity, and spreads laterally for some distance along the interior of the wall. In other forms this internal tissue is more developed, and may even be prolonged into trabeculae, comparable to some extent with those of *Isoëtes*. It has been suggested by Bower,[1] that these extensions of the sterile tissue into the cavity of the sporangium may have served to facilitate the nutrition of the developing spores, and may also have contributed to the mechanical support of the sporangial wall. Both points may well have been of importance in spore-sacs of such large size, with so slender an attachment to the subtending leaf.

In *Lepidostrobus oldhamius* and some other forms,

[1] "Studies in the Morphology of Spore-producing Members," Part i., *Phil. Trans.* B, 1894.

only the small spores are known with certainty. They are present in countless multitudes in each sporangium, and are usually found still grouped in fours, with a tetrahedral arrangement. The spores are very minute, about .02 mm. in diameter. From the analogy of other cones of Lepidodendreae there is a strong presumption that *L. oldhamius* was heterosporous, like *Selaginella*, the microspores alone having been identified at present. Several forms are known to have been heterosporous, and it is most probable that all *Lepidostrobi* will prove to be so when we have a more complete knowledge of the strobili.[1] Fragments of a heterosporous cone, with large megaspores nearly a millimetre in diameter, have been found in the same beds which have yielded the specimens of *L. oldhamius*.

We will, however, choose as our example of heterospory in *Lepidostrobus* a cone from a lower horizon, named *Lepidostrobus Veltheimianus*, a small species which is very abundant in the plant-bearing beds of the Calciferous Sandstones, near Burntisland, in Scotland. These cones are indistinguishable from those of *Lepidodendron Veltheimianum*, one of the few *Lepidodendra* which have been found with the fructification still attached to the branches. As this species is extremely abundant in the Calciferous Sandstone series, of which the Burntisland beds form part, it is extremely probable that the cones with structure preserved belong to it. Hence I have ventured to use the specific name *Veltheimianus* for the cones also. For information

[1] In certain cases, the apparently homosporous strobili were doubtless the male fructifications corresponding to the "seed-bearing" cones of *Lepidocarpon*, described below, p. 193.

on this subject I am indebted to Mr. R. Kidston, F.R.S.[1]

This strobilus is only about 1 cm. in diameter, and was probably not more than 4 cm. in length. In general morphology and structure it is essentially similar to *L. oldhamius*, but all the parts are on a smaller scale, and the slender stele of the axis has but little pith (see Fig. 72). The sporophylls have the

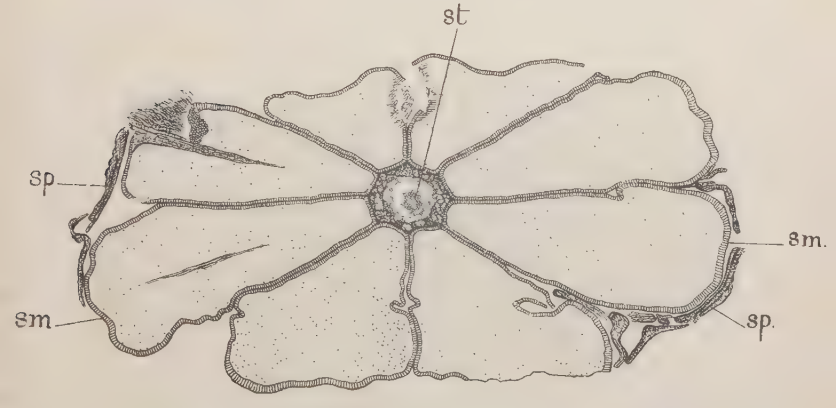

FIG. 72.—*Lepidostrobus Veltheimianus.* Transverse section of cone, through microspore-region. *st.*, stele of axis; *sp.*, laminae of sporophylls (only partially shown); *sm.*, microsporangia; in the two to the left trabeculae are shown. × about 7. S. Coll. 400. (G. T. G.)

same general form as in the previous species (Fig. 74), but the pedicels on which the sporangia are seated are relatively flatter and wider. In some, at least, of the specimens, their arrangement is in alternating verticils. The heterospory is beautifully shown in several specimens; from the longitudinal sections it is

[1] This *Lepidostrobus* was described and figured by Williamson in his "Organisation of the Fossil Plants of the Coal-measures," Part iii. 1872, and Part xix. 1893, *Phil. Trans.*

evident that all the upper part of the cone was occupied by microsporangia, and the lower by megasporangia, as in most species of *Selaginella* at the present day (Fig. 74). Fig. 72 represents a transverse section from the upper, and Fig. 73 one from the lower part of the cone; the former shows microsporangia, the latter megasporangia only.

The structure of the sporangium is similar to that of

FIG. 73.—*Lepidostrobus Veltheimianus.* Transverse section of cone, through megaspore-region. *sp.*, sporophylls (only partially shown); *sm.*, megasporangia; *ma.*, the spinose megaspores. × about 7. S. Coll. 413. (G. T. G.)

the last species; the wall consists of narrow prismatic cells, sometimes divided by a transverse septum. From the base of the sporangium a radial plate of tissue runs up into the cavity, and often forks into two above. This structure may be compared with the trabeculae of *Isoëtes*. It is best shown in the microsporangia, but evident traces of it are present in the megasporangia also. The microspores occur in immense numbers in their sporangia, and are generally found united tetrahedrally in fours. They are of small size, not exceeding

about .02 mm. in diameter. The megaspores are relatively of enormous dimensions, so that they are easily visible to the naked eye. Their mean diameter

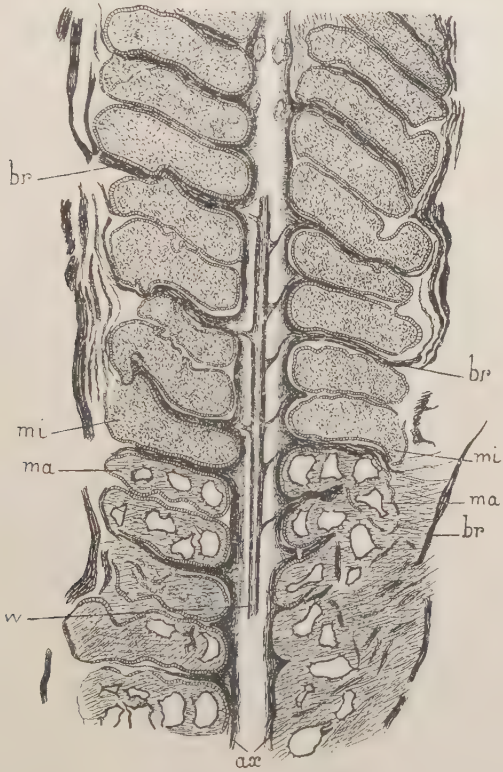

FIG. 74.—*Lepidostrobus Veltheimianus.* Longitudinal section of cone, showing microsporangia above and megasporangia below. *ax*, axis of cone, showing stele (*w*) and leaf-traces, passing out to sporophylls, *br*; *mi*, microsporangia; *ma*, megasporangia, containing a few spinose megaspores. × about 4. S. Coll. 1008. (G. T. G.)

is at least .8 mm., quite forty times that of the microspores (see Fig. 75, C). The number of megaspores in each sporangium was small, certainly not more than sixteen, and perhaps as few as eight (cf. Figs. 73 and

74). The thick membrane of the megaspores was

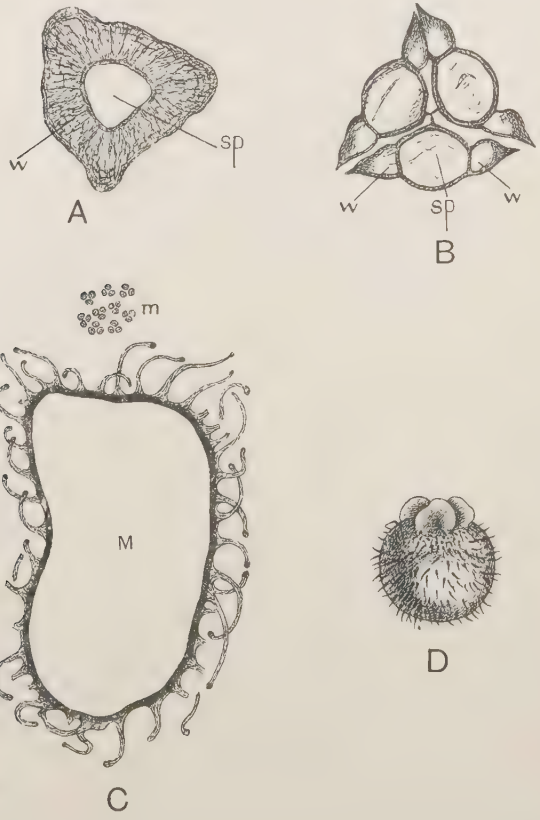

FIG. 75.—Spores of Lepidodendreae. A. *Spencerites insignis*. Spore, showing wing in surface-view. *sp*, cavity of spore; *w*, wing. B. Tetrad, in section, showing three out of the four spores, tetrahedrally arranged. *sp*, cavity of spore; *w*, wing. A and B × about 90. C. *Lepidostrobus Veltheimianus*. M, a single megaspore, showing the blunt spines; *m*, tetrads of microspores, on the same scale. × about 70. After Williamson, *Phil. Trans.* D. A single megaspore, probably of *L. Veltheimianus*, showing spines and lobes of membrane, surface-view. × 15. After Kidston and Bennie.

prolonged on the outside into a number of stout curved spines (see Figs. 73, 74, and 75, C). Detached mega-

spores of *Lepidostrobus* and allied fructifications are very abundant in the Carboniferous formation, and show a great variety in size and surface-sculpture. Some of these megaspores (which were investigated by Messrs. Kidston and Bennie) appear to be identical with those of *Lepidostrobus Veltheimianus*; in addition to the spines, these detached specimens show a curious three-lobed appendage to the membrane of the spore (see Fig. 75, D), which very commonly appears in the sections also. It is probable that this structure, which was of very general occurrence in the megaspores of Lepidodendreae, formed a passage for the admission of the microspores or of the spermatozoids produced by them. Microspores are often found entangled among the bristles of the megaspores.

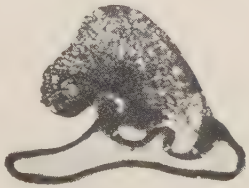

Fig. 76.—*Lepidostrobus foliaceus.* Megaspore (somewhat collapsed) bearing large episporic appendage. × 28. From R. Scott, *New Phytologist.* S. Coll. 1217.

The megaspores of *Lepidostrobus foliaceus*, a Coal-measure species, of which until recently only the microsporangia were known, appear to have numbered not more than four in each sporangium, and possess a curious episporic appendage, comparable to the so-called "swimming apparatus" of *Azolla*[1] (see Fig. 76).

In favourable cases the prothallus is preserved within the megaspore. This is sometimes the case in *L. Veltheimianus*, as is well shown in Fig. 77; the prothallus is here almost complete, and fills the megaspore. Fig. 78, from a photograph, represents

[1] R. Scott, *New Phytologist*, June 1906.

the megaspore and prothallus from a fructification, provisionally named *Mazocarpon*, distinguished by the

FIG. 77.—*Lepidostrobus Veltheimianus*. Megaspore in section, filled with prothallus, which protrudes somewhat through the opening of the megaspore-wall. ×50. S. Coll. 912. R. S.

fact that the megaspores in the sporangium are embedded in a massive parenchymatous tissue. In other specimens traces of the archegonia are recognisable. M.

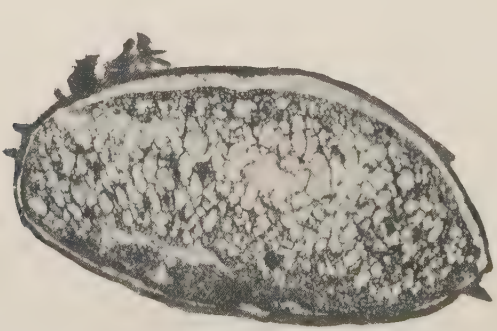

FIG. 78.—*Mazocarpon*, Benson in MS. Isolated megaspore filled with prothallus. × about 35. From a photograph by Mr. W. Tams. S. Coll. 1756.

Renault found megaspores of a *Lepidostrobus* in which the prothalloid tissue contains flask-shaped cavities, strongly suggestive of archegonia.

There is thus every reason to believe that the mode

of reproduction in many of the Lepidodendreae agreed closely with that of the heterosporous Lycopods of the present time, but certain other fructifications of the same group attained, as will be explained below (§ 4), a much higher organisation.

3. *Spencerites.*—The chief generic character of *Lepidostrobus*, distinguishing it from most other Lycopodiaceous strobili, is to be found in the great radial elongation of the sporangium, and its attachment by a long and narrow insertion to the upper surface of the sporophyll-pedicel throughout its length. There is another form of Lycopodiaceous cone from the Coal-measures, which differs in this, as well as in other important points, from *Lepidostrobus*, and which has therefore been separated, under the name of *Spencerites*.[1] This type will now be shortly described, and the description will be based, in the first instance, on *Spencerites insignis* (Will.), the smaller of the two known species.

The strobilus, which is from 8 to 10 mm. or more in diameter, is pedunculate, the peduncle bearing scattered bracts. The sporophylls are in some cases arranged in regular alternating verticils, of about ten members each, though a spiral arrangement has also been met with. As Miss Berridge has shown, the sporophyll consists of a narrow pedicel, about 2.5 to 3 mm. long, carrying an upturned lamina with a broad fleshy base. The lamina

[1] See Scott, "On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks, ii. On *Spencerites*," a New Genus of Lycopodiaceous Cones, *Phil. Trans. Roy. Soc.* vol. 189, B, 1897. The earlier papers by Williamson are there cited. See also Miss E. M. Berridge, F.L.S., "On two New Specimens of *Spencerites insignis*," *Annals of Bot.* vol. xix. 1905.

is produced into a thick dorsal lobe below, and a larger ventral lobe above (see Fig. 79). The sporangia are not elongated, but ovoid or spherical, and not in any way attached to the pedicel, but inserted, by means of

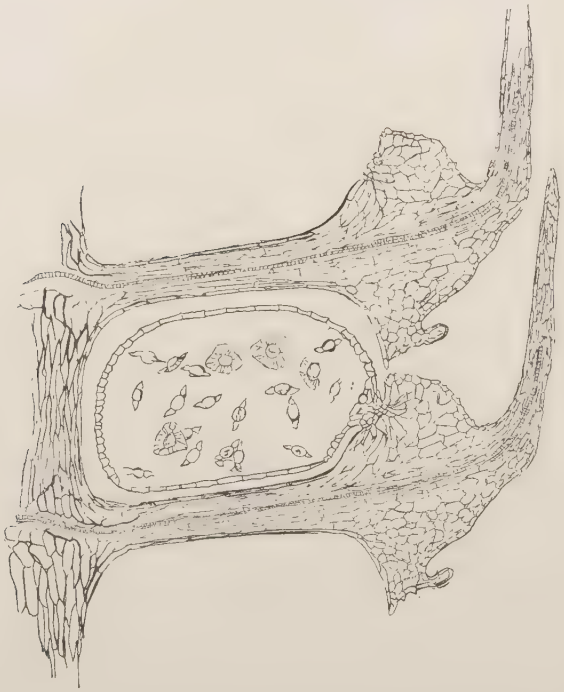

FIG. 79.—*Spencerites insignis.* Somewhat diagrammatic radial section showing two of the sporophylls in connection with the axis. On the lower sporophyll the sporangium is seen, attached at its distal end to the ventral outgrowth; a few of the winged spores are shown. After Miss Berridge.

a short stalk at the distal end, on the upper surface of the ventral lobe (Fig. 79). No ligule has been observed. The structure of the sporangial wall is also quite different from that of *Lepidostrobus*, for it consists of prosenchymatous cells, elongated in the plane of the

wall, and not at right angles to it as in the former genus.

The winged spores are a remarkable feature of the cone (Fig. 75, A and B). They measure about .14 mm. in maximum diameter (not reckoning the wing), and are thus intermediate in size between the microspores and megaspores of a *Lepidostrobus*. They are often found still grouped in tetrads, with a tetrahedral arrangement (Fig. 75, B). Around the equator of each spore runs a broad, hollow, annular wing, formed by the dilation of the cuticle (Fig. 75, A and B). It is probable that this wing served the same purpose as the well-known air-sacs of the pollen-grain in *Pinus* and some other Coniferae, namely to facilitate dispersal by the wind. The form of the air-chamber is, however, quite different, for in *Spencerites* it constitutes a continuous rim all round the spore (Fig. 75, A), while in the Conifer it forms two distinct sacs, one on each side of the pollen-grain. These spores are thus quite unlike anything known in *Lepidostrobus*, and at once distinguish *Spencerites insignis* from allied fructifications.

Indications of a tissue, or of distinct cells, are frequently found in the cavities of the large spores, but there is reason to suspect that these appearances were caused by the presence of some parasitic organism. No signs of microspores have been detected, and so the homosporous or heterosporous character of the strobilus remains uncertain.

The anatomy of the axis is of a simple Lycopodiaceous type, with an axial strand of centripetally developed wood; in some specimens there is a small pith, which is quite absent in others. The leaf-trace

bundles passed out more horizontally than in *Lepidostrobus*, having a somewhat arched course in approaching the pedicel. The inner cortex and, in some cases, the phloëm are preserved: the middle cortex has often disappeared, but when present sometimes shows a remarkable structure, consisting of interwoven trabecular filaments, connected with the inner and outer tissues, and with the sheaths of the outgoing vascular bundles. The outer cortex consists of fibrous sclerenchyma, either continuous or forming a network, with a more delicate tissue occupying the meshes through which the leaf-traces passed out to the sporophylls.

The other species, *S. majusculus*, which is larger, has relatively still shorter sporophylls; as regards the form and insertion of the sporangia, the two species of *Spencerites* agree, but the spores themselves are smaller in *S. majusculus*, and of different shape, having the form of quadrants of a sphere, with narrow wings along the angles. Vegetative stems are known, which in structure much resemble the axis of the *Spencerites* cones. They are of the Lepidodendroid type, and have something in common with the stems of *Bothrodendron* (see p. 200).

The insertion of the sporangium by its distal end on a ventral lobe of the sporophyll suggests a comparison with Sphenophyllales, but the absence of any vascular supply to this lobe in the case of *Spencerites* is a serious point of difference.

Lepidostrobus and *Spencerites* are typical Lycopodiaceous strobili, as to the affinities of which no doubt can arise. The well-marked heterospory of some species (possibly of all) shows that these fructifications had

reached at least as high a differentiation as the most highly organised Lycopods of the present day. They differ most strikingly from recent strobiliferous forms in the mode of insertion of the sporangia, which in existing Lycopodiaceous cones are either axillary (*Selaginella*), or are seated on the sporophyll, close to the axis [1] (*Lycopodium* and *Phylloglossum*). In *Lepidostrobus*, as in the recent, non-strobiliferous *Isoëtes*, the enormous development of the sporangia is due chiefly to radial elongation, and this brings with it a corresponding extension of the base of the sporangium, which is attached to the long pedicel of the sporophyll from end to end. The displacement of the ligule, as described above, affords a good measure of the radial extension of the whole organ. The presence in some cases of trabeculae was no doubt an adaptation to the great bulk of the sporangium.

4. *The Seed-like Lycopodiaceous Fructifications.*—We can well understand that an enormous output of spores must have been necessary in the *Lepidostrobi*, in so far as they were heterosporous. For fertilisation and the development of an embryo to take place, it was essential for microspores and megaspores to germinate together, and where these cones were borne on trees, and often at a great height above the ground, the chances must have been enormously against such an association. The successful accomplishment of the reproductive act could only be ensured by the production of a prodigious number of spores, and especially of microspores. It

[1] *Psilotum* and *Tmesipteris* are left out of consideration, as it is quite doubtful whether the synangium of these genera is comparable to a single sporangium of the typical Lycopods. See Chapter XIV.

is quite probable, however, that the bristles and other appendages of the megaspores may have served to catch the microspores, and thus secure their presence when dispersal took place.

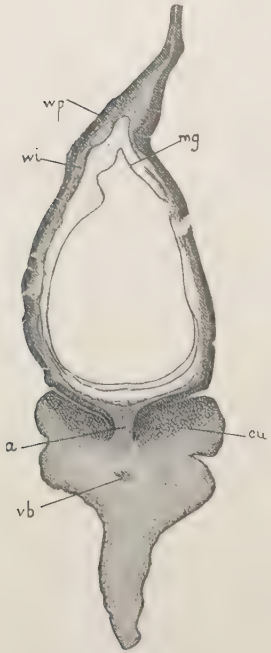

FIG. 80.—*Lepidocarpon Lomaxi*. Sporangium and sporophyll before integument was formed, in tangential section of cone. *cu*, lateral cushions of sporophyll; *a*, base of sporangium; *vb*, vascular bundle; *wp*, palisade layer of sporangium; *wi*, inner layer of wall; *mg*, membrane of megaspore or embryo sac. This section does not pass through the abortive spores. × about 12. (G. T. G.) Scott, *Phil. Trans.* S. Coll. 607.

Recent discoveries have shown that the difficulty was met, in some of the Palæozoic Lycopods, in another way, namely, by the formation of a kind of ovule or seed, which may probably have been fertilised, or at least pollinated, while still on the plant. In *Lepidocarpon Lomaxi*, a cone so closely allied to *Lepidostrobus* that male specimens were formerly regarded by myself and others as a mere variety of *L. oldhamius*, each megasporangium contains a single mature megaspore or embryo-sac, filling almost the whole cavity (Fig. 80), but accompanied by three abortive spores, so that the original number in each sporangium was no doubt four, of which one gained the upper hand over the rest. Around the sporangium, the wall of which was identical in structure with that of a *Lepidostrobus*, the tissue of the bract grew up to form a regular integument, closing

in at the top, but leaving a narrow crevice or micropyle (Figs. 81 and 82). This opening, however, differed from the micropyle of ordinary seeds in not being tubular, but forming a long narrow slit, extending in the radial direction almost the whole length of the sporangium,

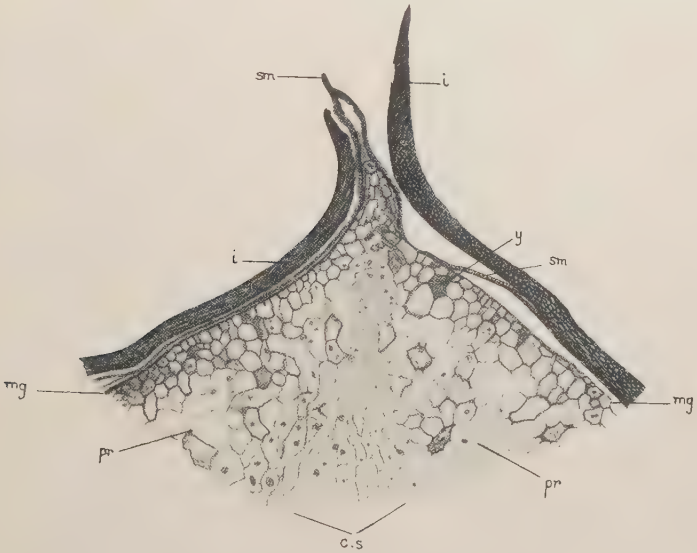

FIG. 81.—*Lepidocarpon Lomaxi.* Upper part of integumented "seed," containing prothallus. *i*, integument; *sm*, wall of sporangium; *mg*, membrane of megaspore; *pr*, tissue of prothallus; *y*, possible central cell of an archegonium; *c.s*, central strand of prothallus. × 20. (G. T. G.) Scott, *Phil. Trans.* S. Coll. 1073.

which was radially elongated, as in an ordinary *Lepidostrobus*. A ligule was present, at the distal end, just as in that genus.

When cut at right angles to this slit-like micropyle, the appearance of the sporangium with its integument is altogether that of a seed (see Fig. 82), and detached specimens were long known to science under the

name *Cardiocarpon anomalum* of Williamson [1] (not of Carruthers). The seeds, which attained a great size, became detached, together with the remains of the sporophyll, and in this condition were never suspected of belonging to a Lycopod until their origin had been traced. The prothallus within the megaspore is not uncommonly preserved (see Figs. 81, 82), and is found in the younger stage, before the integument has grown up, as well as in the mature "seeds." The tissue of the prothallus may show a considerable amount of differentiation (see Fig. 81); only doubtful traces of archegonia have so far been observed.

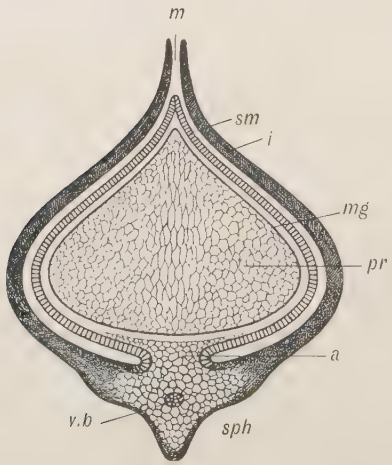

FIG. 82.—*Lepidocarpon Lomaxi*. Diagrammatic section of "seed," tangential to cone. *sph*, sporophyll; *v.b.*, vascular bundle; *i*, integument; *m*, micropyle; *sm*, wall of sporangium; *a*, base of sporangium; *mg*, membrane of megaspore; *pr*, prothallus. (G. T. G.)

In a microspore-bearing strobilus, probably belonging to *Lepidocarpon Lomaxi*, the microsporangia were also provided with integuments, less developed than those of the megasporangiate cone.

Lepidocarpon Lomaxi, and other undescribed species, belong to the Lower Coal-measures; the closely similar

[1] "Organisation, etc.," part viii., *Phil. Trans.* 1877, p. 254, Figs. 117-119; part x. 1880, p. 518, Fig. 64. The identification of these "seeds" with the *Cardiocarpus* of Brongniart is certainly incorrect.

L. Wildianum is frequent in the more ancient Burntisland deposits of Lower Carboniferous age.

The cone of *L. Lomaxi* was first discovered by the late Mr. G. Wild and Mr. J. Lomax, working independently.[1]

Lepidocarpon no longer stands alone among Palæozoic Lycopods in possessing organs analogous with true seeds. Another instance is afforded by *Miadesmia membranacea*, the vegetative organs of which were discovered by Bertrand in 1894 in the calcareous nodules of the English Lower Coal-measures. The stem is very slender, and the plant appears to have been of herbaceous habit. The stele is of simple structure, with centripetal wood and no pith; the cortex contains trabeculae comparable to those of *Selaginella*. The leaves appear to have been borne in four rows; the ligule is remarkably well developed, and the lamina is fringed by a membrane one cell thick, breaking up into uniseriate hairs at the margin. Within the last few years a megasporangiate fructification has been discovered, which is shown, by the structure of the ligule, the fringed margin of the sporophyll, and other characters, to have belonged to *Miadesmia*.[2] The fructifications are borne in a rather lax strobilus. Each sporophyll bears a megasporangium, attached to its upper surface at the proximal end, containing a single megaspore, filling its cavity (Fig. 84). As in *Lepidocarpon*,

[1] See their note "On a New *Cardiocarpon*-bearing Strobilus," in the *Annals of Botany* for March 1900; for the full description see Scott, "On the Seed-like Fructification of *Lepidocarpon*," *Phil. Trans. Roy. Soc.* vol. 194, B, 1901.

[2] Miss M. Benson, "On a New Seed-like Lycopodiaceous Fructification," *New Phytologist*, vol. i. 1902. For the full paper see *Phil. Trans. Roy. Soc.* B, 1908.

the megasporangium is enclosed in an integument, which in *Miadesmia*, however, completely roofs in the sporangium above, leaving only a narrow opening or micropyle at the distal end (Figs. 83 and 84). The integument is provided with long tentacles, which, as they project beyond the micropyle, may probably have assisted pollination. The sporangial wall is less developed than in *Lepidocarpon*, the integument having, as it appears,

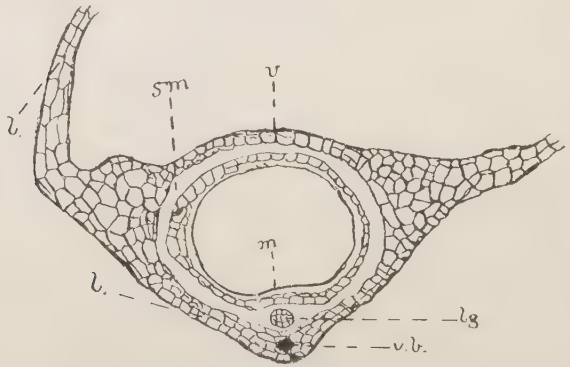

FIG. 83.—*Miadesmia membranacea*. Approximately transverse section of seed-like organ. *l*, *l*, lamina of sporophyll; *v.b.*, vascular bundle; *v*, velum or integument; *lg*, ligule; *sm*, sporangium-wall; *m*, membrane of megaspore. × about 30. R. S. S. Coll. 2237.

more completely taken over the function of a protective organ, and no abortive sister-cells of the single megaspore (in which the prothallus is sometimes present) have been observed. Thus the seed-like character is even more striking in *Miadesmia* than in *Lepidocarpon*. There seems to be no near affinity between the two genera, which differ widely, especially in the insertion of the sporangium and the position of the micropyle, and in each of which, presumably, the seed-habit was independently evolved.

In both genera the most important difference from true seeds, such as those of the Pteridosperms, consists in the fact that the sporophyll as a whole formed part of the seed-like organ, and was shed together with it. In other respects—the single megaspore, the integument, and the indehiscent character—the analogies with seeds are complete. In the case of *Miadesmia* the wide lamina of the sporophyll gave the organ the character of a winged seed.

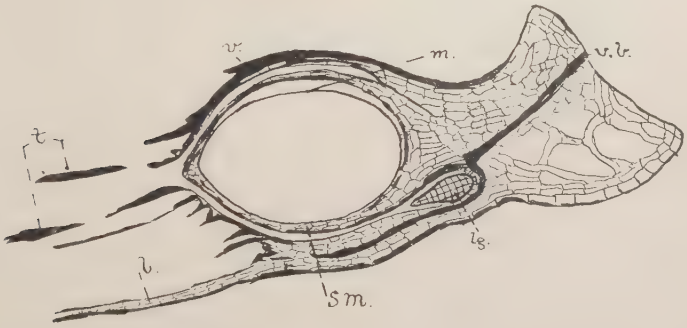

Fig. 84.—*Miadesmia membranacea.* Radial section of seed-like organ. *t*, tentacles; other lettering as in Fig. 83. × about 30. R. S. S. Coll. 2240.

5. *Bothrodendron.*—The genus *Bothrodendron*, of Lindley and Hutton, represents another group of Palæozoic Lycopods, very near *Lepidodendron*, though differing from it in the surface-characters of the stem. The genus is now well known, and presents several points of interest. On the larger stems, the surface of the cortex is smooth, the leaf-scars are very small, and flush with the surface, for leaf-cushions were not developed. This causes a striking difference in appearance from *Lepidodendron*, though the leaf-scars are in themselves quite similar to those of that genus, showing

the usual three prints on the actual scar, with the ligular pit above. On the younger twigs the foliage is sometimes preserved; the leaves are small, and resemble those of a recent *Lycopodium*. The smooth character of the stem-surface has suggested a comparison with a group of the *Sigillariae*, which we shall consider in the next chapter; some authors have even united these two genera.

The stem of *Bothrodendron punctatum* is commonly found in the Ulodendroid condition, bearing the large, cup-shaped scars described in the last chapter. It has, therefore, been inferred that its cones were in these cases borne on the old wood, but in other species they have been found in connection with small twigs, and it has become very doubtful whether the large *Ulodendron* scars really had any relation to the cones. The strobili borne on the slender branches in *B. minutifolium* are identified by Mr. Kidston with a *Lepidostrobus* described by M. Zeiller under the name of *L. Olryi*, a small cylindrical cone with verticillate sporophylls. On the whole, there is no reason to doubt the very close affinity of *Bothrodendron* with *Lepidodendron*.

The group is of great antiquity, chiefly occurring in the lower beds of the Carboniferous formation, while one species has been described from the Upper Devonian of Ireland.

Bothrodendron is thus among the oldest known genera of Lycopods, and it is therefore of much importance that its internal structure should be recognised. This has recently been discovered by Mr. J. Lomax, who finds that a stem showing the characteristic

external features of a *Bothrodendron* has the anatomical structure of the *Lepidodendron mundum* of Williamson.[1] The structure of *Bothrodendron mundum*, as the species may now be provisionally named, is of a simple Lepidodendroid type. In the larger stems there is a massive pith, surrounded by a comparatively thin zone of centripetal wood with well-marked protoxylem groups; in the more minute twigs, however, the xylem is solid. A characteristic feature is the radial arrangement of the primary tissue of the outer cortex, quite apart from the subsequent formation of periderm. No secondary wood has been observed in the stem, but in a *Stigmaria* described by Professor Weiss, probably belonging to the same plant, extensive secondary growth took place (see p. 257).

Still more recently Mr. D. M. S. Watson[2] has identified the cone of *Bothrodendron mundum* in structural material. The cone is a small one, less than a centimetre in diameter, and is hermaphrodite, with the microsporangia above and the megasporangia below. The sporophylls are short in the radial direction, and the sporangium is attached by a narrow neck of tissue to the middle of the horizontal portion; there is a large ligule in the usual position. Each megasporangium was found to contain only four megaspores, which are characterised by their long branched spines. The cone is evidently quite distinct from a *Lepidostrobus*, though apparently nearer to that genus than to *Spencerites*.

Bothrodendron is further of interest from the extra-

[1] "Organisation of Fossil Plants of Coal-measures," Part xvi., *Phil. Trans. Roy. Soc.* B, 1889.

[2] "The Cone of *Bothrodendron mundum*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. lii. Part i. 1908.

ordinary mode of preservation in which one of the species, *B. punctatum*, occurs. At Tovarkovo, in the province of Toula, in Central Russia, beds of a peculiar kind of coal, called leaf-coal or paper-coal, have long been known. The seams are about 8 inches thick, and lie near the surface of the ground, only covered by sand. The so-called coal has all the appearance of a bed of excessively thin dead leaves, intermixed only with structureless organic matter of the nature of humic acid. The leafy films, on investigation, have proved to consist entirely of layers of cuticle, belonging to the stems of ancient plants, from which all other tissues had rotted away, ages before. The cuticles are perfectly fresh and pliable, and not in any way fossilised, although geologists are agreed that the bed (which covers an area of many square miles) belongs to the Carboniferous Limestone horizon, in the lower part of the Carboniferous formation. The cuticle is in some cases complete, corresponding to the whole circumference of the stem which it once enclosed ; it is perforated by numerous small round holes, regularly disposed, and corresponding in arrangement with the leaf-traces of a *Bothrodendron*. The cuticularisation had evidently extended to a portion of the vertical cell-walls abutting on the outer skin, for the network of cells is marked out with perfect clearness on the inner surface of the cuticle. Irregular borings, which occur here and there in the membrane, were attributed by M. Renault to the activity of Palæozoic Bacteria.

The cuticles, when freed from the formless organic matter adhering to them, are of a light brown colour ;

they swell up in water, can be stained with aniline dyes, and on chemical analysis prove to have much the same composition as the cuticle of recent plants. That a vegetable tissue should thus have come down to us, fresh and unaltered, from a period more ancient than that of the Coal-measures, is certainly one of the most remarkable among the curiosities of palæontology.[1]

[1] See Renault, *Les cuticules de Tovarkovo*, Autun, 1895.

CHAPTER VII

LYCOPODIALES—*continued*

Sigillaria and Stigmaria ; Lycopoditeae

I. SIGILLARIA

WE now come to the great genus *Sigillaria*, one of the most extensive and important groups of Palæzoic plants, and one of those of which the affinities have been most keenly discussed. In geological range the *Sigillariae* are somewhat more restricted than the *Lepidodendra* ; they have not been detected with certainty below the rocks at the base of the Carboniferous formation, and scarcely extend above the Permian ; they attain their maximum in the Middle and Upper Coal-measures.

1. *Habit and External Characters.*—The *Sigillariae* must have been among the largest trees of the Palæozoic forests. A trunk of *Sigillaria reniformis*, found near Saarbrücken, in Germany, *in situ*, was 6 feet in diameter at the base, where its roots were attached. This trunk was only 18 feet high, diminishing towards the top to a diameter of about a foot. Other gigantic specimens have a very different form. M. Zeiller[1] describes a

[1] *Bassin houiller de Valenciennes, flore fossile*, p. 512.

trunk found at L'Escarpelle, near Valenciennes, in France, which was traced for a distance of 22 metres (over 70 feet). At the lower end it had a diameter of 60 cm. (about 2 feet), which at the upper extremity had only diminished to 50 cm. (1 foot 8 inches). The stem was thus a slender, nearly cylindrical shaft. Both this and other, even longer, trunks, reaching a length of 30 metres (nearly 100 feet) were unbranched. In some cases the large stems are found still clothed with leaves in their upper part. Thus M. Grand'Eury[1] describes a stem of *Sigillaria lepidodendrifolia*, which, for a distance of 3 metres (nearly 10 feet) from the top downwards, was covered by rigid and erect linear leaves, more than a metre in length. The foliage of *Sigillaria* is in some cases scarcely to be distinguished from that of *Lepidodendron*, and as we shall see below, the agreement extends to histological structure. The stems of *Sigillaria* are often found connected at the base with their subterranean organs, which we will provisionally call roots, though their morphological nature is doubtful, and will have to be discussed later on. These roots (known under the name of *Stigmaria*) are extremely common in the "underclay" of the Coal-measures, immediately below the seams of coal, and no doubt belong to the same plants, the stem and leaves of which have contributed to form the coal itself, the underclay representing the soil in which the trees grew. It is usually, however, impossible to say whether the root-like organs belonged to a *Sigillaria* or a *Lepidodendron*. Fig. 85 shows an enormous specimen of the stumps and roots of one of

[1] *Flore carbonifère du Département de la Loire*, p. 156.

these trees found in a sandstone quarry, of Coal-measure age, at Clayton, near Bradford, in Yorkshire. The actual stump of the tree is here 4 feet 4 inches in diameter, while the whole specimen, including the forked roots, is almost thirty feet across. This gigantic fossil is now set up in the Museum of the Owens College at Manchester, and affords a striking example of the scale of Palæozoic vegetation. Fragments of other

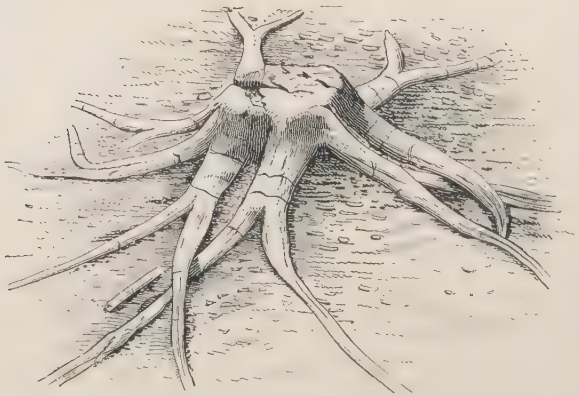

FIG. 85.—Stump and roots (= *Stigmaria ficoides*) of a Lycopodiaceous tree from the Coal-measures. For description, see text. After Williamson.

specimens, which must have been about twice the size of this one, were found at the same time.

Before going further into the question of the habit of the Sigillarian trees, it will be necessary to give some account of the characteristic superficial markings, by which the genus is commonly recognised, and according to the variations in which, the so-called "species" are distinguished.

Sigillaria, like *Lepidodendron*, is characterised by the form and arrangement of the leaf-scars, left on the

surface of the stem after the leaves themselves had fallen. The wonderful perfection with which these markings are often preserved, even on large trunks, is certainly a surprising fact, and seems to show, either

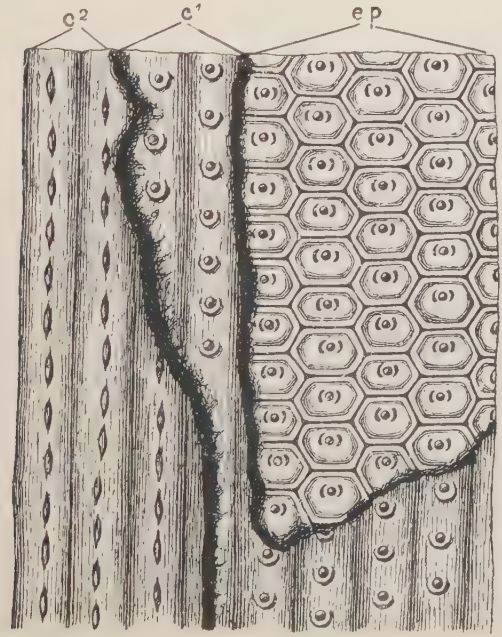

FIG. 86.—*Sigillaria tessellata.* Surface of stem. *ep*, external surface, showing leaf-scars, with the prints of the vascular bundle and parichnos; c^1, sub-epidermal surface; c^2, deeper cortical surface, showing "*Syringodendron*" characters. Nat. size. After Schimper.

that the growth of the trees was extremely rapid, or that the Carboniferous forests were singularly free from epiphytic or parasitic vegetation.

The leaf-scars of *Sigillaria* are, as a rule, arranged in conspicuous vertical series, the scars of adjacent series alternating with one another (see Figs. 86-89). The

marked longitudinal seriation of the scars affords, in typical cases, the most obvious distinction from the sculpturing of *Lepidodendron.* The scars are not always seated on distinct leaf-cushions, or if such cushions are present, they are not much larger than the scars themselves (Fig. 86). The individual leaf-scar has, as a rule, an approximately hexagonal outline, with the angles more or less rounded (see Figs. 86-89). The form

FIG. 87.—*Sigillaria mamillaris* (*Rhytidolepis* type). Surface of stem, showing vertical ribs with leaf-scars (*l.s.*) and scars of the cones (*c.s.*). Nat. size. After Zeiller.

of the scar varies much, not only in different species, but on different parts of the same stem; as the stem increased in diameter with age, the scars not only became more widely separated, but were also themselves stretched out in the horizontal direction.

The prints on the scar are essentially similar to those of *Lepidodendron*, and are here also three in number, forming a transverse row, usually a little above the centre of the scar (see Fig. 88). The middle print,

which is dot-like, or transversely elongated, is the smallest, but the most important, for anatomical investigation has shown that this alone represents the vascular bundle of the leaf. The two lateral prints are vertically elongated, and are either straight or crescent-shaped, with the concavity directed inwards. These lateral marks are of the same nature as the parichnos of *Lepidodendron*. Immediately above the scar, and sometimes seated in a depression of its upper edge, is another print, which evidently represents the ligular pit (Fig. 88, *lg*). We thus see that, except for trifling details, there is no difference in morphology between the leaf-scars of *Sigillaria* and those of *Lepidodendron*.

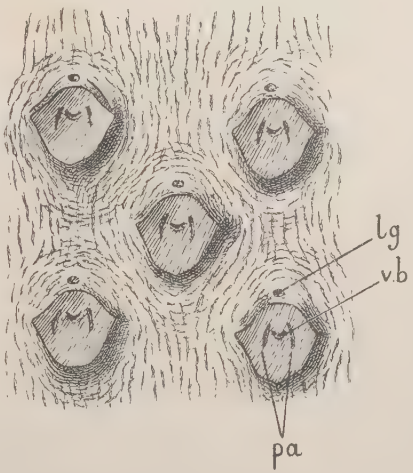

FIG. 88.—*Sigillaria Brardi* (*Leiodermaria* type). Part of surface of stem, showing five leaf-scars. *lg*, ligule; *v.b.*, print of vascular bundle; *pa*, parichnos. × 1½. After Weiss.

When we come to the arrangement of the scars, we meet with considerable variations within the genus; these variations have been used for the distinction of subgenera, which some authors have even erected into distinct genera. We shall see, however, that in the light of our present knowledge very little, if any, taxonomic value can be attached to these differences, though they are worth noting for descriptive purposes.

In the first instance, the genus *Sigillaria* has been divided into two main series, those with ribbed stems—the *Eu-Sigillariae*, and those without ribs—the *Sub-Sigillariae*. The ribs, characterising the former series, are broad longitudinal ridges, each of which bears a single vertical series of leaf-scars. The ridges are separated by comparatively narrow furrows (Figs. 86 and 87).

The *Eu-Sigillariae* were formerly divided into two subgenera, *Rhytidolepis* and *Favularia*—names which, though no longer of taxonomic significance, may be retained to designate types of surface. In *Rhytidolepis* the ribs, which are often much broader than the leaf-scars borne upon them, are separated by straight vertical furrows. The scars of the same vertical series are in some cases almost contiguous; more often they are separated by considerable spaces (see Fig. 87). The ribs have been looked upon as representing series of fused leaf-bases, a view, however, which is negatived by the observations of Arber and Thomas, who find that the true leaf-bases form bracket-like projections from the ribs, the latter being really part of the cortex. *Rhytidolepis* is the most characteristic form of *Sigillaria*, and the most remote in outward appearance from *Lepidodendron*. The great ribbed stems of this type are a striking and familiar feature of the Coal-flora, and are among the best-known fossil remains.

The other ribbed type of surface—termed *Favularia* by Sternberg—has the ridges separated by zigzag furrows, while a marked transverse furrow intervenes between the adjacent leaf-scars of the same series (see Fig. 86). Here, in fact, each scar is seated on a well-

marked hexagonal leaf-cushion, though the arrangement in vertical series is still manifest. The extreme forms of *Rhytidolepis* and *Favularia* are distinct enough, but both may occur on different parts of one and the same stem, connected by intermediate forms, so no systematic value can be attached to the distinction. Generally speaking, the *Eu-Sigillariae* are geologically more ancient than the *Sub-Sigillariae*, and some of the oldest stems known show the *Favularia* type of surface.

The *Sub-Sigillariae*, which are characteristic of the Upper Coal-measures and Permian, agree in the absence of distinct ribs, and have likewise been grouped under two subgenera, to which the same remarks apply as in the case of the previous group. In the *Clathraria* of Brongniart, the surface of the stem is formed by somewhat prominent, contiguous leaf-cushions, separated by oblique furrows, each cushion bearing the scar of a leaf (see Fig. 89, which, however, is too much like a *Favularia*). Here the oblique parastichies stand out more conspicuously than the vertical orthostichies, and there is a certain approach to the *Lepidophloios* form of surface, from which, however, the typical *Clathraria* differs in the greater size of the scar relative to the cushion, and in the form of both.

In the other division of *Sub-Sigillariae*, the *Leiodermaria* of Goldenberg, there are no prominent leaf-cushions; the scars are remote from each other, and separated by a smooth cortical surface (see Fig. 88). This form shows some approximation to *Bothrodendron*, which has even been united with this group of *Sigillariae* by some recent authors. The Clathrarian and Leiodermarian sculpturings may both occur on the

same stem—in fact, the characteristic markings of the type-species of *Clathraria* and *Leiodermaria* respectively, *S. Brardi* and *S. spinulosa*, have repeatedly been found associated in this way. The two forms of surface frequently occur in alternating zones on the stem, and the same is the case with the *Rhytidolepis* and *Favularia* markings among the *Eu-Sigillariae*. It has been suggested that the crowded leaf-scars characteristic of *Favularia* and *Clathraria* may have coincided with periods of slow growth, while the more scattered arrangement in the *Rhytidolepis* and *Leiodermaria* forms may have been due to seasons of rapid elongation. All these four types, however, have been regarded, even by some modern authors, as distinct genera. As a matter of fact, only the division between *Eu-Sigillaria* and *Sub-Sigillaria* holds good taxonomically, and even here the distinction is not always a sharp one, for some forms of Favularian and Clathrarian [1] surface approach each other very nearly,[2] and may even occur on the same stem.

A hundred or more so-called species of *Sigillaria* have been described, according to the superficial markings, but they are admittedly of doubtful value at the best. The genus, however, was evidently a rich and varied one, though the characters available are altogether insufficient for the clear limitation of the different forms.

Just as in *Lepidodendron*, so also in *Sigillaria*, the appearance of the stem was often much changed by the partial destruction of the external tissues, and the various

[1] Clathrarian *Sigillariae* are also spoken of as *Cancellatae*.

[2] On the subject of the surface-characters of *Sigillariae*, see Zeiller, "Revue des travaux de Paléontologie," *Rev. gén. de botanique*, 1897, p. 404; *Éléments de Paléobotanique*, Paris, 1900, p. 190.

types of more or less decorticated surface noticed under *Lepidodendron* recur here. One very characteristic form may be noticed, to which the name *Syringodendron* has been given. In this, the epidermis and the leaf-scars have perished; the ribs—if the specimen belonged to the *Eu-Sigillariae*—remain, and are marked by the same prints which occur in the typical leaf-scars. In these cases, the middle print—that marking the leaf-trace bundle—is usually inconspicuous, while the two lateral lines of the parichnos are extremely marked. Corresponding forms of preservation, without the ribbing, occur in the *Sub-Sigillariae*. The *Syringodendron* character may also be found, even on the epidermal surface, at the base of the old stems, where excessive growth in thickness has obliterated the leaf-scars. Fig. 86, from *Sigillaria tessellata*, one of the Favularian forms, shows the surface exposed at three different levels. At *ep* the natural epidermal surface is shown, with the characteristic hexagonal leaf-scars, each of which shows the three prints (representing the vascular bundle and the double parichnos) as described above. On the part marked c^1, the superficial layers, with the leaf-scars, have peeled off, exposing the outer cortex, on which the longitudinal ribs come out more clearly than before. The leaf-trace bundles are still evident; the two parichnos-scars have united below each vascular bundle, forming a crescent. At c^2 the process of destruction has gone deeper; a considerable thickness of cortex has broken away, and a deeper layer is laid bare. The ribs are still evident; the fused parichnos-scars show conspicuously as lenticular outlines, but the vascular bundle within each loop is not visible. This lowest level may

be taken as representing the *Syringodendron* surface, though on a small scale. In typical *Syringodendron* the parichnos-prints may be enormously enlarged, reaching a length of more than a centimetre.

In some cases the leaf-scars on the Sigillarian surface are accompaned by other scars, usually regarded as marking the insertion of the fructifications (see Fig. 87, *c.s.*). We will, however, postpone the consideration of these, until we come to deal with the cones themselves.

As regards the habit of the *Sigillariae*, our knowledge is still very imperfect. In some of the forms, forking branches have been observed, though they are not as a rule common ; in stems with the *Rhytidolepis* type of sculpturing no branching has yet been observed. In the unbranched forms the habit appears to have been something like that of the Australian Grass-tree, *Xanthorrhoea*, the tall, upright shaft terminating in a sheaf of long, grass-like leaves. In other cases, as in the Favularian species *S. elegans*, and in *S. Brardi*, of the *Clathraria* group, the stem divided, by successive dichotomy, into a few large branches.

2. *Anatomical Structure.*—Recognisable specimens of *Sigillaria* with structure preserved are comparatively rare ; of late years, however, several new examples have come to light. It is possible that the rarity of specimens with structure, while the structureless casts are so common, may be in part due to the smaller branches not having always been recognised as belonging to *Sigillaria*. The fact, however, would also find an explanation, if branching occurred very sparingly, for,

of course, the small branches, rather than the great trunks, are likely, as a rule, to have been preserved in the petrified condition.

The first specimen of a *Sigillaria* showing anatomical structure was described by Brongniart,[1] as long ago as the year 1839, and has played a most important part in the history of fossil botany. The fragment was about 4 cm. in diameter, and about 2 cm. long, and showed a portion of the external surface with its leaf-scars, as well as the internal anatomy (see Fig. 89). The superficial characters have rendered it possible to identify the specimen as belonging to the form *Sigillaria Menardi*, one of the *Clathraria* group.[2] The parts in which the structure is preserved consist essentially of the wood and a portion of the outer cortex ; the pith and the inner region of the cortex have perished (see Fig. 89). Fortunately, however, the parts which remain are the most important, as Brongniart pointed out. His whole description, though nearly seventy years old, might still serve as a model for such investigations. The ring of wood is complete, and has a diameter of about 16 mm. The pith was of large size, for the woody zone is only about a millimetre in thickness. It consists of a large number (between forty and fifty) of vascular bundles, each of which is made up of an inner or primary and an outer or secondary portion. The primary strands are distinct from each other, though close together, and are crescent-shaped, as seen in transverse section, with

[1] "Observations sur la structure intérieure du *Sigillaria elegans*," *Archives du muséum d'hist. nat.* vol. i. 1839.

[2] Brongniart himself referred the specimen to the Favularian species, *S. elegans*, but this determination was subsequently corrected by Zeiller and Renault.

the convex side towards the pith. The small, spiral tracheides are placed on the outer, slightly concave, side of each bundle. The rest of the primary xylem-elements, which are irregularly arranged, and increase

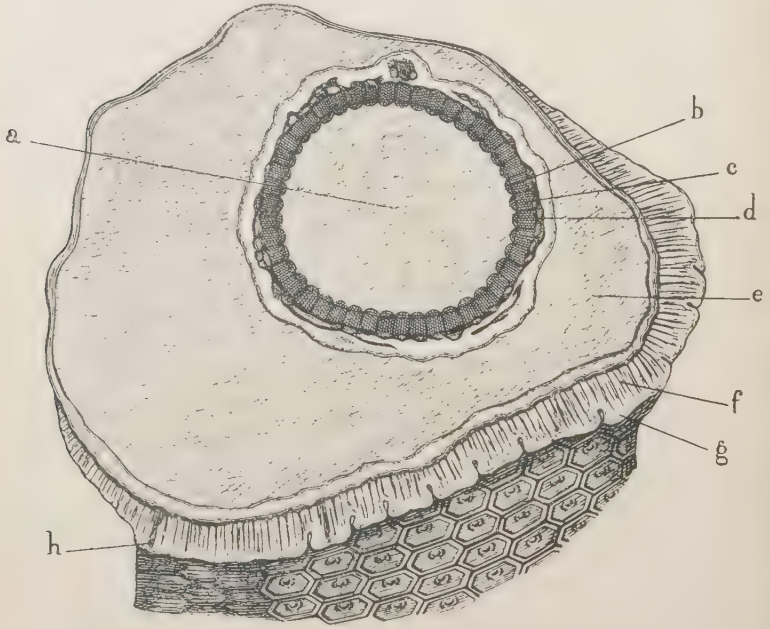

FIG. 89.—*Sigillaria Menardi* (*Clathraria* type). Brongniart's original specimen, showing transverse section and part of surface with leaf-scars. *a*, pith (perished); *b*, primary wood, forming many distinct bundles; *c*, secondary wood; *d*, phloëm-zone; *e*, middle cortex (perished); *f*, periderm; *g*, leaf-base; *h*, foliar bundle. × about 2. After Brongniart.

in size towards the interior, are reticulated or finely scalariform tracheides.

The secondary zone, which is almost continuous, though showing some signs of division into distinct bundles corresponding to the primary strands, consists of radially arranged scalariform tracheides, and narrow

medullary rays of very variable height. The interfascicular rays seem to have been only slightly broader than those opposite the primary bundles. The secondary tracheides, as in the Lepidodendreae, are pitted on their tangential as well as on their radial surfaces; the smallest elements lie towards the interior, adjacent to the protoxylem of the primary strands.

The leaf-trace bundles, so far as their xylem is concerned, were given off from the outer, concave part of the primary strands, and passed obliquely through the secondary wood; the preservation only allows of their being traced for a short distance beyond the woody zone. M. Renault finds that these leaf-trace bundles are "diploxylic," each consisting of an inner centripetal primary strand, and an outer centrifugal secondary portion continuous with the secondary wood of the stele. This character was long regarded as peculiar to *Sigillaria*, as distinguished from *Lepidodendron*, but the distinction no longer holds good, for it is not constant in *Sigillaria*, while, as already mentioned in Chapter V., Prof. Seward and Mr. Hill found typical "diploxylic" leaf-traces in a fine specimen of *Lepidodendron Wunschianum*, a plant which may belong more properly to *Lepidophloios*, but is, at any rate, not a *Sigillaria*. This structure is shown in Fig. 57, p. 142.

The outer cortex, which is alone preserved, consists of two zones; the more internal is composed of uniform, radially arranged tissue, and no doubt represents a secondary formation, of the nature of periderm, such as we so constantly find in *Lepidodendron*. The outer zone, bearing the leaf-cushions, is simply the primary

external cortex, within which the periderm had formed (Fig. 89, *f* and *g*).

If we compare the structure of *Sigillaria Menardi* with that of the Lepidodendreae with secondary thickening, such as *L. Wunschianum* or *L. brevifolium*, we find one difference of importance. The primary wood in the Lepidodendreae forms a continuous zone, usually of considerable thickness, while that of *Sigillaria Menardi* is less in amount, and is broken up into a ring of distinct and definite bundles. The latter difference is striking enough, but, as we shall see, it does not serve to distinguish *Sigillaria* generically.

The inference which Brongniart himself drew from the study of the structure of his *Sigillaria* was this: "The arrangement of the woody tissue in bundles composed of radial series is a character foreign to all the Cryptogams; it is, on the contrary, characteristic of the Dicotyledons";[1] and hence he was led to conclude, "that the *Sigillariae* and *Stigmariae* constituted a special family, entirely extinct, probably belonging to the great division of Gymnospermous Dicotyledons."[2] This conclusion, which was natural enough at that time (1839), still has an historical interest, owing to the dominant influence which the views of this great investigator long exercised, especially in his own country. The force of Brongniart's argument is now, of course, entirely invalidated by the discovery of a great number of Cryptogams with secondary growth, and by our knowledge of the Cryptogamic fructification of *Sigillaria* itself.

In 1875 MM. Renault and Grand'Eury described

[1] "*Sigillaria elegans*," p. 440. [2] *l.c.* p. 447.

some specimens of another *Sigillaria* showing internal structure;[1] the superficial characters of the stem enabled them to identify it as belonging to the Leiodermarian form *S. spinulosa*; the latter, however, as mentioned above, is now known to have been identical with the Clathrarian *S. Brardi*, so there is no important distinction, so far as external characters are concerned, between Renault's and Brongniart's species. Some authors, indeed, have even united *S. Menardi* with *S. Brardi*, in which case the two French observers would have been dealing merely with varieties of the same species. The anatomy, however, appears to negative this view; the two species are probably distinct, though nearly allied.

In the case of *S. spinulosa* several specimens were available for investigation, from branches of various sizes. The primary wood is of about the same thickness as in the former species, but shows curious variations in its arrangement. At some points it is broken up into distinct bundles, quite similar to those of *S. Menardi* (see Fig. 91), but elsewhere, even in the same transverse section, it forms a continuous band for a considerable distance (see Fig. 90).[2] We thus see that the separation of the primary xylem-zone into definite strands is not necessarily a character of any taxonomic importance. The primary wood was centripetal, and agrees in minute structure with that of *S. Menardi*. The secondary zone (which in some of

[1] "Étude du *Sigillaria spinulosa*," *Mém. prés. par divers savants à l'Académie des Sciences*, tome xxii. 1875.

[2] For the photographs reproduced in these two figures I have to thank my friend Mr. Kidston, who took them from sections of one of the original specimens.

the specimens attains a thickness of about 2 cm.) is here perfectly continuous, but otherwise agrees closely

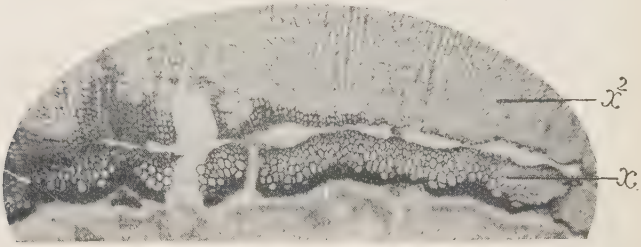

FIG. 90.—*Sigillaria spinulosa.* Part of transverse section of stem, showing primary (x) and secondary (x^2) wood. The former consists partly of separate and partly of confluent bundles. × about 9.

with that of the former species. The leaf-traces arose, in this case also, at the outside of the primary wood,

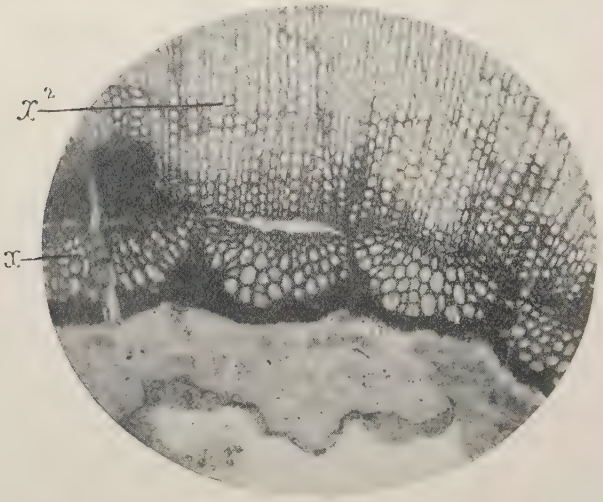

FIG. 91.—*Sigillaria spinulosa.* Part of wood, more highly magnified, showing separate primary strands (x) and secondary wood (x^2). × about 18. Figs. 90 and 91 from photographs by Mr. R. Kidston, F.R.S.

passed through the secondary zone, and then took a nearly vertical course through the inner cortex, which

is partially preserved in these specimens. In the outer cortex the bundles assumed a more horizontal direction. In some of the sections they show a diploxylic structure. In this species M. Renault first made the interesting observation that two large lacunae accompanied the bundle on its outward course, one on each side, forming, at the point where they entered the leaf, the two lateral prints on the foliar scar, which are now termed the parichnos. In this and in other species of *Sigillaria* M. Renault subsequently showed that the lacunae, which are surrounded by a definite sheath of radially elongated cells, were filled by a delicate cellular tissue traversed by secretory canals (see Fig. 92, A). The same observer also proved, by anatomical investigation, that the well-known prints on the partially decorticated *Syringodendron* stems are of the same nature, though here much enlarged. The identity of *Syringodendron* with *Sigillaria* thus received fresh demonstration.[1]

In *Sigillaria*, as in *Lepidodendron*, the parichnos-strands start from the inner cortical zone. That their function was in part secretory is highly probable, but the persistence and enlargement of the parichnos on the surface of old stems suggests a respiratory function, like that of lenticels.

The outer cortical layers of *S. spinulosa* have a peculiar structure. There is a broad zone of secondary periderm, but its tissue is not uniform; it is made up of radial anastomosing bands of narrow elongated cells, while the meshes between these bands are occupied by

[1] See also E. H. Coward, "On the Structure of *Syringodendron*, the Bark of *Sigillaria*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. li. Part ii. 1907.

short thin-walled cells of greater diameter. As the fibrous bands, which no doubt had a mechanical

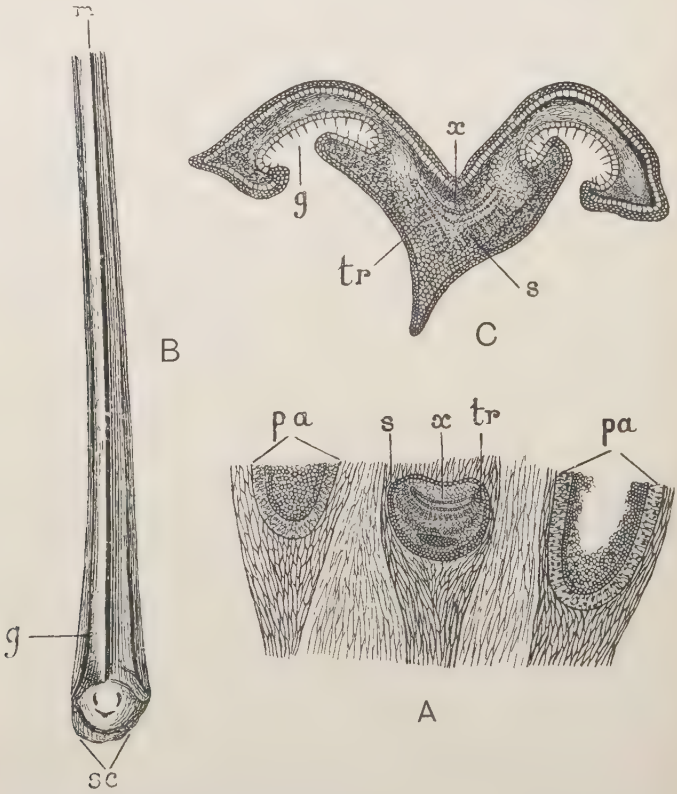

FIG. 92.—A and B, *Sigillaria spinulosa*. A. Tangential section of outer cortex, showing leaf-trace, with the parichnos (*pa*) on either side. In the leaf-trace; *x*, primary xylem; below this the secondary xylem (*tr*) and phloëm, then a sclerenchymatous strand; *s*, sheath of bundle. Magnified. B. Leaf, showing the lower surface, and the scar (*sc*) at base; on the scar the prints of the bundle and parichnos are seen. *m*, midrib of leaf; *g*, one of the stomatiferous furrows. Nat. size. C. *S. latifolia*. Transverse section of leaf. *x*, xylem; *s*, sclerenchyma; *er*, transfusion-tissue; *g*, stomatiferous furrows, lined with hairs. Magnified. All after Renault.

function, fuse with each other in every direction, they form a network, whether seen in tranverse or tangential

section. The existence of this highly differentiated secondary cortex, so distinct from the uniform periderm of *S. Menardi*, certainly seems to justify the specific separation of these two forms, even if there were no other diagnostic characters. The fibrous periderm attained an immense development; fragments 7 or 8 cm. thick are found, and these appear to be only exfoliated laminae of a much thicker bark.

Beyond the secondary cortical zone lies the primary outer cortex, bearing the leaf-bases, where they are preserved. The interest of this species lies chiefly in two points—the transition which it shows between continuous and discrete primary xylem, and the complex character of the secondary cortical zone.

Both in *S. spinulosa* and *S. Menardi* the structure of the leaf-bases has been made out, thanks once more to M. Renault's researches. Towards the exterior of the cushion there is a rather thick-walled hypoderma; the softer tissue within contains the two parichnos-strands already described, and between them lies the vascular bundle (cf. Fig. 92, A). The primary wood forms a narrow transverse band, surrounded by a delicate tissue.[1] The secondary wood is separated by this tissue from the primary xylem; it forms an arc of radially arranged elements towards the lower side of the bundle. Below this again is a layer of phloëm. Some light is thrown on this peculiar arrangement of the parts of the bundle by the structure of the leaf

[1] M. Renault regarded this as primary phloëm, which may be correct, as in the leaf the transfusion-tissue (apparently continuous with the secondary xylem) lies outside the primary phloëm. See *Flore fossile d'Autun et d'Épinac*, Part ii. p. 212.

itself, which was also thoroughly investigated by M. Renault.[1]

The leaves with their structure preserved are in association, but not in actual connection with the stems. In cases, however, such as that illustrated in Fig. 92, B, where the base of the leaf itself shows a characteristic scar, corresponding with those on the stem-surface, there can be no doubt as to the attribution. The general form and structure of the Sigillarian leaf (the species chiefly studied was *S. Brardi*, with its variety, *S. spinulosa*) is much like that of a *Lepidodendron*. Here also there are two deep longitudinal furrows on the lower surface, one on either side of the midrib, and it is only on the surface of these furrows that the stomata are found (see Fig. 92, C, *g*). The single vascular bundle appears to have been concentric in structure, the xylem having its spiral elements placed laterally. Below the bundle itself is a double layer of sclerenchyma, beyond which is a band of delicate parenchyma with scattered tracheides. This accessory xylem may be regarded as corresponding functionally to the transfusion-tissue of Coniferous leaves. We have already described the same tissue in the leaves of *Lepidodendron*, where, however, the extra-fascicular tracheides are more abundant, and form a complete zone round the bundle. The transfusion-tissue of the Sigillarian leaves was at first regarded by M. Renault as secondary xylem, but he afterwards withdrew that view, considering that the true secondary wood is limited to the leaf-trace, where it passes through the cortex of the stem. It seems,

[1] *Flore fossile d'Autun et d'Épinac*, Part ii. p. 213, Plate xli.

however, to be clear that the secondary xylem and the transfusion-tracheides are continuous one with another; the relations of the tissues require further investigation.

The mesophyll is lacunar in the neighbourhood of the stomatiferous furrows; elsewhere it is described as consisting of transversely elongated elements, which may have enabled the leaf to roll up its lamina, and thus diminish transpiration. There is a band of sclerenchyma below the epidermis, except in the stomatiferous furrows. The stomata are of the ordinary kind; they are accompanied on the epidermis of the furrows by multicellular hairs (Fig. 92, C, *g*). The whole arrangement of the tissues of the leaf is suggestive of a plant occasionally exposed to drought, but we must remember that the plants of salt marshes assume in many respects a xerophytic habit.

It will be seen that the leaves of the species of *Sigillaria* in question agree nearly, though not exactly, in structure with those of *Lepidodendron*, as described above in Chapter V. The differences between them are such as are often found even among species of the same genus; the resemblances, taken in conjunction with the other characters, are undoubtedly indicative of near affinity.

It appears probable that the leaves of *Sigillaria* were separated from the stem by the formation of a definite abscissile tissue.

So far we have dealt exclusively with the structure of the Sub-Sigillarian group. Our knowledge of the anatomy of the *Eu-Sigillariae* has until recently been extremely meagre, but is now much augmented. A fragment of stem with Favularian surface was described

by Williamson[1] in 1871, but except as proving the presence of a secondary zone of wood, and of a periderm, the investigation yielded little result. The same author described at the same time, under the name of *Diploxylon*, a vascular cylinder which he afterwards referred to *Sigillaria reniformis*, one of the *Rhytidolepis* group (*l.c.* Figs. 33 and 34). In this stem there is a perfectly continuous zone of primary wood, with a crenulated outer margin, beyond which is a much broader layer of secondary xylem. The first really good English example of a stem of the *Rhytidolepis* type, with structure preserved, was a specimen which came several years ago into the hands of Professor Boyd Dawkins, and has not yet been fully described.[2] The specimen is a fragment only, forming a segment of the stem, but it includes the whole thickness of the tissues from the pith to the outer surface (Fig. 93). The latter is ribbed in the characteristic manner of *Rhytidolepis*, and there appears to be no doubt of its belonging to a *Sigillaria* of that type. From the inner margin of the wood to the exterior surface of the ribs the radius of the specimen is about 18 mm. The zone of primary xylem, which is less than a millimetre in thickness, is quite continuous as far as it can be traced. Its outer edge, where the smallest elements are placed, is crenulated, just as in Williamson's specimen, referred to above. The secondary zone of wood, which has the usual structure, is about 4 mm. thick, and has an undulating outer surface, corresponding to the crenula-

[1] "Organisation of Fossil Plants of Coal-measures," Part ii. 1872.

[2] For photographs of this specimen, one of which is reproduced in Fig. 93, I am indebted to Mr. A. Gepp of the British Museum, Natural History Department.

tions of the primary zone. This latter character may serve to distinguish a *Sigillaria* from a *Lepidodendron*, but too much stress must not be laid on it. The inner cortex is imperfectly preserved ; the outer bark consists chiefly of a thick zone of radially seriated periderm (Fig. 93, *pd*), beyond which a narrow band of primary cortex (*c*) abuts on the surface of the ribs. The leaf-traces are ranged in vertical rows corresponding to the

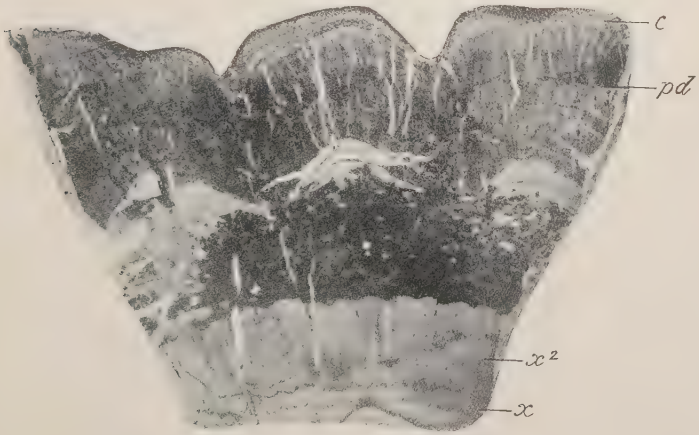

FIG. 93.—*Sigillaria* (*Rhytidolepis* type). Segment of stem, in transverse section, including three ribs. *x*, crenulated primary wood ; x^2, secondary wood ; *pd*, periderm ; *c*, outer cortex. × 3. From a photograph by Mr. A. Gepp.

ribs of the cortex. The xylem-strands of the leaf-traces start from the *depressions* of the crenulated primary wood, just as in *Sigillaria Menardi* or *spinulosa*, and in Williamson's specimen mentioned above. It is thus evident that each concave segment of the continuous primary wood, in the *Rhytidolepis* type of stem, corresponds to one of the distinct bundles, as shown in the Sub-Sigillarian forms previously described.

A more perfect specimen of the stem of a ribbed

Sigillaria (probably *S. elongata*), from the Hardinghen coal-field, in the Pas de Calais, has been described by Professor C. E. Bertrand (*Annals of Botany*, December 1899). His more complete observations agree essentially with the short account just given of an English specimen. Professor Bertrand points out that the ribbed *Sigillaria* is in certain respects intermediate in structure between the *Sub-Sigillariae* and the *Lepidodendra* with secondary growth.

More recently Mr. Kidston has given a full account of the structure of a petrified specimen of *Sigillaria elegans* from the Lower Coal-measures of Yorkshire.[1] This is a Favularian species ; the characteristic leaf-scars are shown quite plainly on the surface of the specimen. The structure of the stele is essentially the same as in the form already described, and here also the leaf-traces invariably start from the base of the furrows of the crenulated primary wood. The medullary rays are one cell thick, and of varying height ; their cells, as in *Lepidodendron*, sometimes show scalariform markings The leaf-trace has a distinctly mesarch structure, and is without any secondary xylem. The structure of the bodies known as "cone scars" shows them to be the bases of small lateral branches, which may well have borne the fructifications (see p. 214).

Quite lately the structure of certain species of the *Rhytidolepis* group has been investigated by Kidston and by Arber and Thomas[2] in material from the

[1] Kidston, "On the Internal Structure of *Sigillaria elegans*," *Trans. Roy. Soc. of Edinburgh*, vol. xli. Part iii. 1905.

[2] Kidston, "Prelim. Note on Internal Structure of *Sigillaria mamillaris* and *S. scutellata*," *Proc. Roy. Soc. Edinburgh*, vol. xxvii. Part iii. 1907 ; Arber and Thomas, "On the Structure of *Sigillaria scutellata*, etc.," *Proc. Roy. Soc. London*, 1907 (abstract).

Coal-measure nodules. In *S. mamillaris* (see Fig. 87) the structure is almost identical with that of the Favularian *S. elegans*; in *S. scutellata* the crenulations of the primary wood are comparatively slight (Fig. 94). On the whole the wood structure in both is the same as

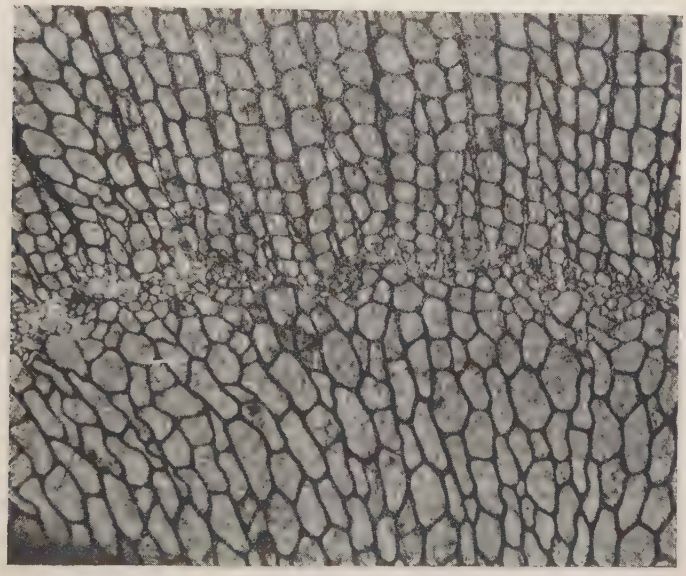

Fig. 94.—*Sigillaria scutellata.*—Transverse section of a portion of the wood, showing primary xylem below and secondary xylem above. The protoxylem-groups lie at the outer border of the primary xylem. × about 50. From a photograph lent by Mr. E. A. Newell Arber, F.G.S. S. Coll. 2300.

that above described. Arber and Thomas find that in *S. scutellata* the periderm was formed on the inner side of a meristematic zone which was active periodically. The ribs consist largely of the phelloderm, but were probably already present in the primary condition of the stem. The authors were able to demonstrate the presence of a ligule and ligular pit on the leaf-base.

The most remarkable point, however, which they observed is, that in traversing the phelloderm the leaf-trace divides into two; in the leaf-base the two xylem-strands are wide apart.

In 1879 Renault described, under the name of *Sigillariopsis Decaisnei*,[1] a small stem, with leaves attached, from the Permian of Autun; the stem resembles that of *Sigillaria Menardi* in structure, but the wood contains pitted as well as scalariform

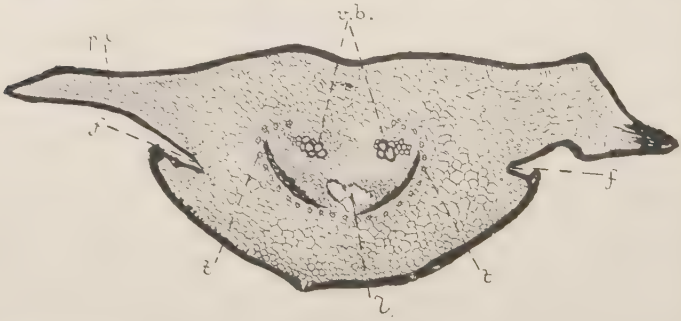

FIG. 85.—*Sigillariopsis sulcata*. Transverse section of leaf. *v.b.*, the xylem-groups of the double vascular bundle; *l*, lacuna, representing secretory tissue; *t*, *t*, transfusion-tissue, forming a horse-shoe, surrounding the double bundle, but open above; *p.t.*, palisade tissue on the upper side and flanks of the leaf; *f*, *f*, stomatiferous furrows. × 22. S. Coll. 2272. R. S.

tracheides; the leaf is traversed by two parallel vascular bundles, which only fuse towards the tip. These characters are altogether exceptional among Lycopods, but in other respects the structure is quite of the Lycopodiaceous type. Leaves occur in the nodules of the British Coal-measures which agree with those of Renault's plant in possessing two distinct vascular bundles, though presenting some specific

[1] *Structure comparée de quelques Tiges de la Flore Carbonifère*, Paris, 1879, p. 270.

differences. In all other respects their structure is that of a Sigillarian leaf (see the details in Fig. 95). The name *Sigillariopsis sulcata*[1] has been given to the English species, for the leaf has two stomatiferous furrows, as in *Sigillaria* or *Lepidodendron*. *Sigillariopsis*, which may correspond to a part of *Sigillaria*, is interesting from its analogies, in certain points, with the structure of some of the Coniferae, with which, however, an affinity is improbable. There is good evidence that the British *Sigillariopsis* was borne on the stem known as *Sigillaria scutellata* (or some closely allied species), in which, as Arber and Thomas have shown, the double leaf-traces are quite similar in structure to the double bundle of the leaf. It thus appears that the *Sigillariopsis* type of leaf probably occurred both on Eusigillarian and Subsigillarian stems. The double bundle is an important character, and may prove to be of generic value.

3. *Fructifications.*—Our examination of *Sigillaria* has shown us, up to the present point, a very close agreement with *Lepidodendron*, as regards the external morphology and the anatomy of stem and leaf. It is, however, on the character of the fructification that the determination of the systematic position of the genus must ultimately depend. This knowledge we owe primarily to M. Zeiller, who in 1884 first demonstrated the nature of the cones of *Sigillaria*.[2] Before that date several specimens had been described as Sigillarian

[1] Scott, "On the Occurrence of *Sigillariopsis* in the Lower Coal-measures of Britain," *Ann. of Bot.* vol. xviii. 1904.

[2] "Cônes de fructification des Sigillaires," *Ann. des sci. nat.* (*Bot.*), ser. vi. vol. xix. 1884.

fructifications, and some, as it has turned out, rightly so, but evidence of identification was not forthcoming. This was supplied by M. Zeiller, for the peduncle of one of the cones described by him is partly clothed by acicular leaves or bracts, and where these have become detached, the leaf-scars are found to lie in vertical rows on the ribbed surface, and to correspond very closely to the markings on the stem of definite species of *Sigillaria*, of the *Rhytidolepis* type. This correlation having once been effected, it became possible to identify various other specimens as cogeneric, and the genus *Sigillariostrobus*, as the fructification of *Sigillaria* is called, now includes several species. The cones are often of large size, reaching a diameter of about 6 cm. (*S. nobilis*) and a great length. None of the French specimens were complete, but Mr. Kidston has since described a complete cone, from the Yorkshire coal-fields, 9 inches long. All the known Sigillarian cones agree in having long peduncles clothed with acicular bracts. The fertile part bears large, crowded sporophylls, arranged spirally, or in alternating whorls. The form of the individual sporophylls varies in the different species; thus in *S. Tieghemi* (which shows *Rhytidolepis* markings on the peduncle) it is broadly lanceolate and contracted at the base to a narrow claw, so that only a small round scar is left on the axis when the sporophyll has become detached. The short claw is approximately horizontal in direction, while the lamina is bent more or less sharply upwards. In other species, the lamina is prolonged into a fine point, and may be toothed or ciliate at the margins (see Fig. 96, A, from one of the English species discovered by Mr.

Kidston[1]). M. Zeiller was not able to observe the sporangia in any of his cones (with the exception of a doubtful form to be mentioned immediately). In several specimens, however, he found groups of large spores, obviously megaspores, lying on the upper surface of the sporophylls, as if they had been set free by the breaking down of the sporangial wall. Though the specimens were not petrified, and their internal structure was thus not preserved, it was found possible to isolate and carefully examine the carbonised megaspores. They are spherical, and of large size, ranging from 1 to 2.25 mm. in diameter in the various species. The cell-wall generally shows three radiating lines, corresponding, no doubt, to the limits of the sister-cells in the same tetrad. The membrane may either be smooth or echinulate, according to the species.

M. Zeiller has also described a small cone, under the name of *Sigillariostrobus Crepini*,[2] in which the sporangia, but not the spores, can be recognised. In this form, the sporangia appear to be attached at their distal ends to the spoon-shaped laminae of the sporophylls. In dimensions and general organisation this cone agrees very nearly with *Spencerites insignis*, described in the last chapter. The relation of *S. Crepini* to *Sigillaria* is, however, not quite beyond doubt.

The observations of M. Zeiller established the Cryptogamic nature of *Sigillaria*, for the fructifications were clearly those of a heterosporous member of the

[1] Kidston, "On the Fossil Flora of the Yorkshire Coal-field," second paper, *Trans. Roy. Soc. Edinburgh*, vol. xxxix. Part i. 1897.

[2] Zeiller, *Bassin houiller de Valenciennes*, *Flore fossile*, p. 605, Plate lxxvii. Fig. 3.

Lycopodiaceae. Mr. Kidston, in his memoir above cited, has made further important additions to our knowledge of these strobili, for in certain new forms of *Sigillariostrobus*, which he has described, from the Coal-measures of Yorkshire, he has been able to demonstrate the form and position of the sporangia, and to obtain at least indications of the presence of microspores in some of them. The sporangia were observed in longitudinal section on the fractured surface of a specimen which had been split down the middle; for it must be remembered that in no case has an undoubted cone of *Sigillaria* been found with the tissues actually petrified. The sporangia prove to have been oval bodies with their long axis directed radially, and were seated each on the horizontal pedicel of the sporophyll, to which the sporangium was to all appearance attached along the whole of its lower surface (Fig. 96, B). The sporangial membrane also appears, so far as the state of preservation allows us to judge, to have been continuous with

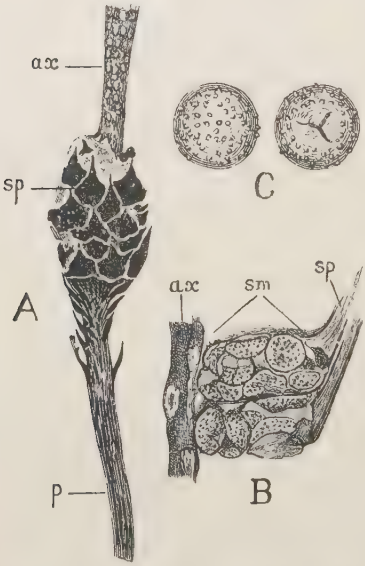

FIG. 96.—A. *Sigillariostrobus rhombibracteatus*, Kidston. Part of cone, showing the pedicel (*p*) with sterile bracts. *sp*, sporophylls; *ax*, axis exposed, showing scars of sporophylls. ⅔ nat. size. B and C. *S. ciliatus*, Kidston. B. Part of axis (*ax*) with sporophylls (*sp*) and megasporangia (*sm*) seen in radial fracture. × 3. C. Echinulate megaspores. × about 7. All after Kidston.

the upturned laminar portion of the sporophyll, or possibly it may have been covered in by an indusium, as in *Isoëtes*. The sporangia contain large megaspores, with an echinulate membrane (see Fig. 96, C). It would appear, therefore, that the sporangia of *Sigillaria*, in their form and mode of insertion, resembled those of *Lepidostrobus*, while differing from those of *Spencerites* or of *Sigillariostrobus Crepini*, which should perhaps be removed from its present genus.

A fine granulation, strongly suggesting the presence of small crowded microspores, was observed by the same investigator in the sporangia of another specimen, which at the same time showed distinct megaspores in other parts. If this indication is to be relied on, it follows that *Sigillariostrobus*, like so many forms of *Lepidostrobus*, bore both kinds of spore on the same cone.

The discovery of the fructification of *Sigillaria* affords an explanation of certain scars which have long been known to occur occasionally on the stems, either between the vertical rows of leaf-scars, or scattered among them in the same series. These scars occur on all forms of Sigillarian stem. Fig. 87 (p. 208) represents them (*c.s.*) on the surface of *S. mamillaris*, which is of the *Rhytidolepis* type. Each scar has a central print, no doubt corresponding to a vascular strand, the structure of which has been demonstrated by Mr. Kidston in the case of *S. elegans* (see p. 228). In one case, small leafy shoots, the dimensions of which agreed well with those of the peduncles of the cones, are said to have been found seated on the scars. It is therefore reasonable to assume that we have in these marks the prints

left by the deciduous cones after their fall. It would follow that the fructification must have been borne on the large stems (for it is on such that the scars occur), and not on small terminal branches. This conclusion is quite in agreement with the unbranched or little-branched character of the Sigillarian stems. The occurrence of Ulodendroid scars on stems referred to Clathrarian Sigillariae (*e.g. S. discophora*) may be mentioned here, though their relation to the cones is open to doubt (see p. 167).

The controversy as to the systematic position of *Sigillaria* has gradually died out since the discovery of the manifestly Cryptogamic fructifications of the genus. The view, long maintained by Brongniart and his school, that *Sigillaria*, or at least the smooth-barked species, belonged to the Gymnosperms, no longer has any basis. The recent discovery of the seed-like fructifications of certain Palæozoic Lycopods might at one time have been used in support of this position, but there is at present no evidence that any of the Sigillariae possessed organs of this kind.

We may take it as now definitely established that *Sigillaria* was a genus of highly developed Lycopodiaceous Cryptogams, having the closest affinities with *Lepidodendron*. The difficulty, in fact, is rather to find constant distinctions between the two genera, than to prove their relationship.[1]

It is not probable that *Sigillaria* had even a remote affinity with the Cycads, the family with which Brongniart and his followers endeavoured to connect it.

[1] The family Lepidodendreae is thus most naturally regarded as including the genus *Sigillaria*.

As we shall see later on, there is strong evidence for tracing the origin of the Cycadales from quite a different Cryptogamic phylum, namely that of the Ferns.

The question of a possible affinity between the Palæozoic Lycopods generally and certain of the Coniferae, an hypothesis advocated by some modern writers, will be considered in the concluding chapter.

II. Stigmaria

1. *Habit and External Characters.*—The subject of the roots or other subterranean organs, both of *Lepidodendron* and *Sigillaria*, has been postponed so far, because it presents considerable difficulty, and we are not even now in a position to distinguish the roots of the one genus from those of the other.[1] Yet *Stigmaria ficoides*, which includes most of the specimens in question, is the very commonest of all fossils in the English Coal-measures, and other strata of similar horizon, and its outward appearance is familiar to every one who has paid the least attention to fossil remains. The *Stigmariae*, which are ordinarily preserved as structureless casts, are long, more or less cylindrical or slowly tapering bodies, varying in diameter from an inch or so up to more than two feet. The surface is marked all over with quincuncially arranged circular scars. Each scar is depressed, with a raised margin; within the scar is a second, much smaller circle, in the centre of which a raised point can be detected in good specimens (Fig. 97). The scars mark the insertion of

[1] The morphological character of these organs is considered below, p. 259. The word "root" is used here in a physiological sense.

the appendages, which are often found *in situ*, radiating out in all directions, and forming approximately a right angle with the main axis (see Fig. 97). The appendages have been found to reach a length of 12 or 15 inches; they have a nearly cylindrical, but gradually tapering form, and are slightly constricted at the base. Their dimensions are small compared with those of the

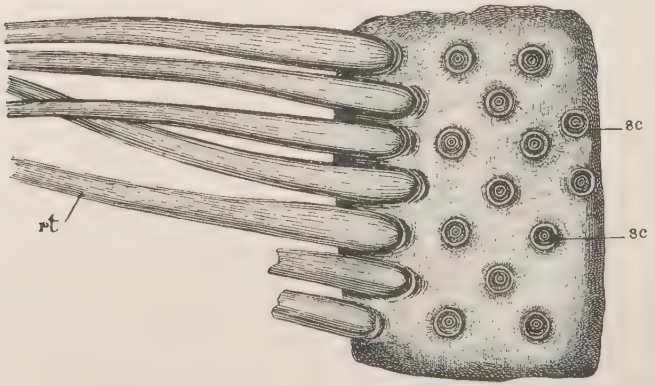

FIG. 97.—*Stigmaria ficoides*. Part of surface, showing the rootlet-scars (*sc*) to some of which the rootlets (*rt*) are still attached. Reduced. After Schimper.

main axis, scarcely reaching a diameter of half an inch, while they are often quite slender.

The main *Stigmariae* themselves attained an immense length; one was traced by the late Prof. W. C. Williamson for a distance of 37 feet 4 inches from its base; in this length it twice forked, but the only branch which could be followed to its full extent measured about 28 feet, from the second dichotomy to its end. At the base of the whole, the diameter was no less than 32 inches, which diminished to a mere point at the extremity of the

long branch. This specimen appears to be the largest *Stigmaria* which has been found in actual connection with the tree-stump to which it belonged; detached specimens have been described of much greater length.

Up to the year 1839 there seems to have been no good evidence as to the nature of *Stigmaria*, though the probability of its being the root of *Sigillaria* was recognised by some investigators, as, for example, by Brongniart. In 1839, during the construction of the Manchester and Bolton Railway, the stumps of several large fossil trees were discovered at Dixon Fold, with four great dichotomous roots radiating from the base of each trunk. The distinctive characters of these trees and their roots, however, could not be determined. A few years later a number of similar trees were found by Binney at St. Helen's and at Dukinfield, in Lancashire. Their trunks showed the characteristic Sigillarian markings, while the branches of the forked roots bore the Stigmarian scars.[1] Thus the proof was first given that *Stigmaria* is identical with the subterranean parts of the Sigillarian trees, a conclusion which has been confirmed by various later observations. Subsequently, other specimens of *Stigmaria* were found in connection with tree-trunks, which showed the markings, not of *Sigillaria*, but of *Lepidodendron*. Specimens of this kind were first observed in the Coal-measures of Nova Scotia, by Richard Brown, soon after Binney's discoveries in England, but there was some doubt as to whether Brown's trees were

[1] See Williamson, "Monograph of *Stigmaria ficoides*," Palæontographical Society, 1886.

rightly identified as *Lepidodendron*. Other cases, however, observed in Germany and in England, seem to leave no doubt that the *Stigmariae* formed the subterranean organs of *Lepidodendron* as well as of *Sigillaria*. It is not even possible to distinguish specifically between those of the two genera; the name *Stigmaria ficoides* does duty for both, and though other species have been distinguished, we are rarely able to correlate their diagnostic characters with those of the stems. One or two special cases, on which rather more light has been thrown, will be mentioned after the common "species" has been dealt with. In the meantime, we may take *Stigmaria ficoides* as representing the "roots" of various *Lepidodendra*, as well as of various *Sigillariae* of the ribbed division.

The mode of connection between the *Stigmaria* and its Sigillarian or Lepidodendroid stem has been shortly noticed above (p. 206, Fig. 85). This has now been observed in a great number of specimens, and the main features appear to be constant. There is never a tap-root forming the direct downward continuation of the vertical stem; the Stigmarian roots are always given off laterally from the base of the stem, and there are always four of them to start with, the four occupying at their attachment the whole circumference of the trunk, which ends abruptly between them; its under surface is marked by a cruciate furrow, corresponding to the lines of junction of the Stigmarian roots. Each of these main roots forked at least twice, and if the first dichotomy took place very near the base, their number may appear to be greater than four. Whether the stem be large or small,

the arrangement is just the same; thus in the Clayton specimen shown in Fig. 85, the stump of the stem is more than 4 feet in diameter, while in another figured by Williamson in his Monograph it only measures 6 inches. The angle at which the Stigmarian roots pass off from the stem is variable. Sometimes they take a nearly horizontal direction from the first; in other cases they first strike sharply down at an angle of 50° or 60°, and only begin to take a more horizontal course at some distance from the main trunk.

The Stigmarian roots, as mentioned above, are especially abundant in the clay underlying the coal-seams, to which the name "Stigmarian clay" has been given by English geologists; they are, however, by no means limited to this position. The conditions must often have been more favourable for the preservation of these underground organs than for that of the aërial stem; hence it is not surprising that in some Carboniferous beds on the Continent, *Stigmariae* are found without any corresponding remains of *Sigillaria* or *Lepidodendron*. It is still uncertain whether *Stigmaria* when living ever occurred except in connection with aërial stems. The *Stigmaria*, with its appendages, manifestly performed the functions of a root, taking up food from the soil. A rich soil seems to have suited it, for the Stigmarian rootlets burrowed in every direction through the mass of decaying vegetation which formed the organic material of the calcareous nodules. They occur in countless numbers, crowded together and penetrating every kind of vegetable fragment—stem, leaf, root, or cone, so that the first lesson a beginner has to learn, in studying the

microscopic structure of coal-plants, is to avoid confusing these intruders with integral parts of the organs which they invade. We may form some idea of the conditions under which the *Stigmariae* grew, from the analogy of weeds growing on a leaf-mould heap, and sending their roots in all directions through the decaying vegetable mass beneath them; only, in the case of the *Stigmaria*, the weeds are represented by gigantic trees. Special care is necessary in the frequent cases where the rootlets led a kind of cannibal existence, burrowing into roots and rootlets of their own kind. Such cases have deceived even practised observers; thus Göppert described an intruding rootlet, found in the pith of a Stigmarian axis, as part of the structure of the latter, and this elementary blunder misled several of his successors, until Williamson set the matter right.

2. *Anatomical Structure.*—We have now to consider the internal structure of *Stigmaria* and its appendages; our description will be based in the first place on the common type *S. ficoides*, which is by far the best known.

The main axis of *Stigmaria* consisted of a well-developed vascular cylinder, surrounded by cortex and periderm (see Fig. 98). The centre of the stele was occupied by a fair-sized pith, the tissue of which is rarely found preserved, except in the outer part, next the wood. Possibly the pith may have been fistular during life. The wood forms a broad zone, divided up into bundles by the principal medullary rays (Fig. 98, *x*). These bundles constantly anastomose laterally with each other, forming a network, in

which the principal rays occupy the meshes. Throughout almost the whole thickness of the woody zone, a regular radial arrangement of the elements prevails; there is no sharp distinction between primary and

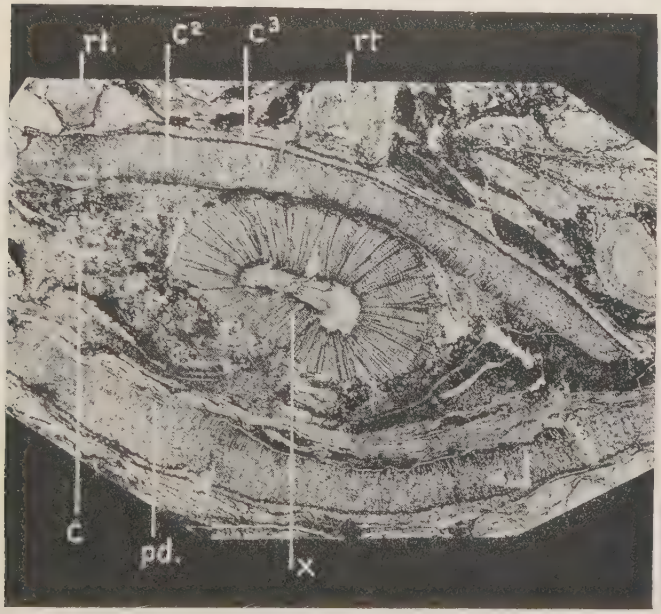

Fig. 98.—*Stigmaria ficoides*. Transverse section of a small specimen. *x*, zone of wood, radially seriated throughout; *c*, middle cortex, only partially preserved; *pd*, periderm; *c²*, outer primary cortex; *c³*, hypodermal zone of cortex; *rt*, bases of rootlets; free rootlets are also shown. × 3½. From a photograph by Mr. L. A. Boodle. Spencer Coll. 147 (now S. Coll. 1465).

secondary xylem, but at the inner end of each wedge the elements are smaller and less regular than elsewhere. Good radial sections show that the spiral tracheides are placed at the extreme inner edge of the wood, next the pith, so that centripetal wood in this form of *Stigmaria* was entirely absent. This is a rather surprising

anatomical peculiarity, considering that the centripetal primary wood is one of the chief structural characters of Lycopods, both recent and fossil. The case of *Stigmaria ficoides* is not, however, without analogy within the Order. Thus, in the creeping stem of *Selaginella spinosa*, the first-formed tracheae are central, so that the whole of the wood is centrifugally developed. The same is the case in the hypocotyl and rhizophores of *S. Kraussiana* and other species.[1] In both plants the upper parts of the axis have the normal structure, with centripetal xylem, just as in the case of the Sigillarian or Lepidodendroid stems to which *Stigmaria ficoides* belonged. As we shall see presently, the absence of centripetal wood does not hold for all forms of *Stigmaria*.

The bulk of the xylem in *S. ficoides* consists of radially arranged scalariform tracheae, the pits occurring on the tangential as well as on the radial walls of the elements (Fig. 99). In addition to the principal rays, numerous narrow secondary rays traverse the wood; they may consist of a single radial row of cells, or may be several cells in height; usually they are one cell thick, sometimes more (Fig. 99, *m.r*). It is an interesting fact that the rays consist partly of spirally or reticulately thickened elements, presumably tracheides, a peculiarity which, as we have seen, is very general in the secondary wood of Lepidodendroid stems. There is here an obvious analogy with the complex organisation of the medullary rays in the Abietineae, though the two structures no doubt arose quite independently.

[1] See the papers by Bruchmann and Harvey Gibson, cited on p. 260.

The regular radial seriation of the secondary xylem-elements is sometimes interrupted by the intercalation of a tangential band of much smaller tracheae, beyond

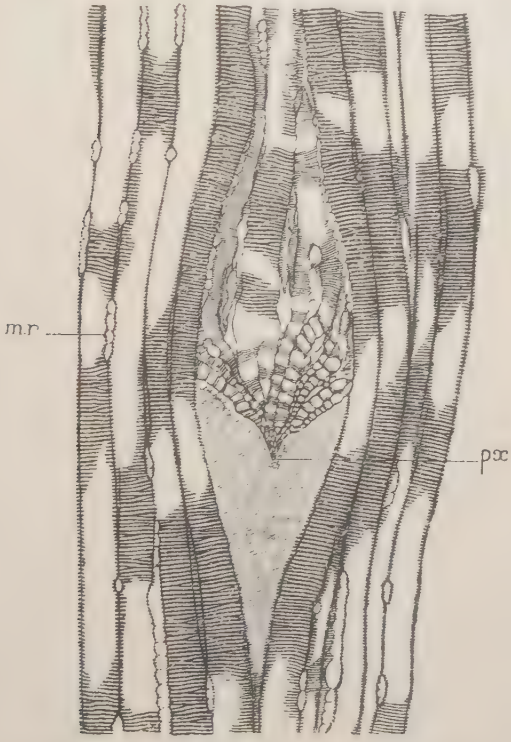

FIG. 99.—*Stigmaria ficoides*. Part of tangential section through wood, showing an outgoing rootlet-bundle. All the tracheides are scalariform. *m.r*, medullary rays; *px*, protoxylem of rootlet-bundle. The top of the figure is directed towards the base of the *Stigmaria*. × 40. Spencer Coll. 150 (now S. Coll. 1469). (G. T. G.)

which the regular formation of large elements recommences. These interruptions no doubt point to a break in the activity of the cambium, but the small-celled layers are not always continuous, and cannot be regarded as marking annual rings. To use Williamson's

words: "The meristemic activity of the cambial layer may have manifested itself irregularly rather than periodically."[1] At the exterior of the wood, some remains of the cambium can sometimes be traced, passing over externally into a zone of delicate tissue, more or less radially arranged, and consisting, as shown by longitudinal sections, of elongated elements. This was no doubt the phloëm. On its outer margin is an imperfectly preserved lacunar zone, such as often occurs in a corresponding position in the stems of *Lepidodendron*. The middle cortex (Fig. 98, *c*) is never perfectly preserved, but where parts of it remain, it appears to have the same curious trabecular structure, as if made up of interwoven filaments, which we so often find in the same region in *Lepidodendron*. In some specimens the preservation of the outer cortex is very perfect (see Figs. 98 and 100). The primary structure of this region can only be observed in fairly young examples (Fig. 98, c^2). Most of its thickness is made up of a very uniform large-celled parenchyma. On the external surface is a hypodermal zone of smaller cells, marked off from the rest of the cortex by a narrow band of dark tissue, probably sclerotic (Figs. 98, c^3, and 100).

Periderm-formation set in early, and the older specimens were provided with an immensely thick bark, fragments of which are among the "common objects" of the coal-balls. The development of periderm (Figs. 98 and 100, *pd*) began in a deep-seated layer of the outer cortex, and appears to have gone on for some time, chiefly in the centripetal

[1] "Monograph of *Stigmaria ficoides*," p. 17.

direction, for it is on the inner edge of the secondary cortical zone that remains of the delicate phellogen can be traced. The tissue thus formed cannot have been of the nature of cork, for the outer tissue shows no sign of withering, and some of its cells had sometimes undergone tangential division, as if starting a

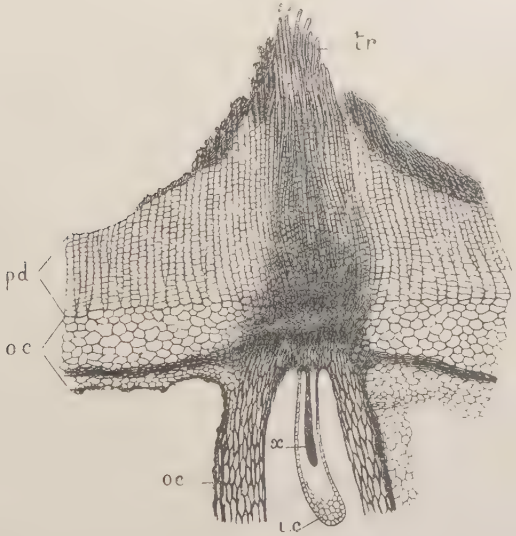

FIG. 100.—*Stigmaria ficoides.* Part of transverse section, to show base of a rootlet. *pa*, periderm of main axis; *o.c*, outer cortex (including hypoderma) of main axis and of rootlet; *i.c*, inner cortex, *x*, xylem of rootlet; *tr*, tracheides passing out to rootlet. × about 15. (G. T. G.)

new, more external phellogen. In many of the Carboniferous plants the formation of secondary cortex played a much more important part than is usually the case in recent vegetation, and though we use the words "periderm" and "bark," it is certain that many of the structures thus indicated were very different in nature and function from the recent tissues which

answer to them morphologically. A characteristic feature of the Stigmarian bark is the great tangential dilatation of the more external peridermal cells.

The above must suffice for a general account of the anatomy of the Stigmarian axis; it remains to describe its appendages, and their relation to the parent organ.

As already mentioned, the appendages, which we will call simply *rootlets*, following Williamson's terminology, are arranged in quincuncial order on all parts of the Stigmarian surface (see Fig. 97). The vascular strand of each rootlet, so far as its xylem is concerned, starts from the inner, primary margin of the wood of the main axis, and bends sharply outwards, taking a nearly horizontal course through the secondary xylem. Every principal ray is traversed by one of these rootlet-bundles, which appear in tangential sections of the axis as tongue-shaped bodies, with the point projecting freely into the lenticular cavity, left by the decay of the ray, while the base is continuous with the adjacent wood (see Fig. 99). The orientation is such that the free point (protoxylem) of the rootlet-strand is directed towards the *apex*, while its connection with the wood is towards the *base* of the main axis.[1] Thus the water absorbed by the rootlet would have been directly conducted through the wood of the main organ, to the aërial stem.

The xylem of the rootlet was increased to some extent with the growth of that of the main axis, for the strand becomes larger as we follow it outwards through

[1] Thus in Fig. 99 the growing point of the *Stigmaria* would have lain in the *downward*, and its base in the *upward* direction, as the figure is drawn.

the secondary wood. In the ill-preserved middle cortex the rootlet-bundles are often met with, and here their course seems to have approached more nearly to the vertical. The parenchyma immediately surrounding the bundle is often preserved when the general cortical tissue has perished. In this region the sectional form of the xylem of the rootlet is triangular, with protoxylem at the apex. At the opposite side the phloëm can sometimes be recognised.

On entering the outer cortex the bundle again takes a more horizontal course. It is here surrounded by a well-marked zone of tissue, in which layers corresponding to the inner and outer cortex of the free rootlet can already be distinguished. In passing through the periderm the parenchymatous tissues of the base of the rootlet kept pace, by tangential divisions, with the growth of the surrounding secondary zone (Fig. 100).

Fig. 100 shows, in longitudinal section, the structure of the rootlet at its base, where it is just escaping from the cortex of the principal axis, which is shown in transverse section. At its attachment, the rootlet is a solid structure with its tissues complete, but as soon as it becomes free the inner and outer cortex are separated by a wide lacuna, in which only slight remains of the probably trabecular tissue, which once occupied it, can be traced. The outer cortex is continuous with that of the main organ, the hypoderma extending over from one to the other without change (Fig. 100, *o.c*). The inner cortex, enclosing the vascular strand, is seated directly on the solid tissue of the transitional region. The continuity of the outer tissues from the main axis to the rootlet appears to prove that

the origin of the latter could not have been endogenous. Probably the rootlets were formed excessively near the apex of the parent organ.

We have now to describe the characteristic structure of the free rootlet, but may first point out how the anatomy of its base exactly accounts for the configuration of the scars on the ordinary Stigmarian surface

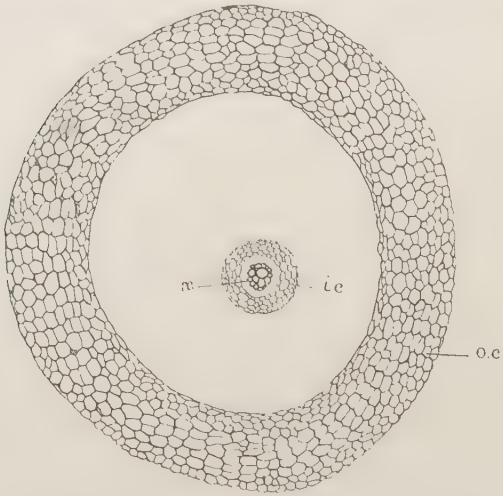

FIG. 101.—*Stigmaria ficoides*. Transverse section of rootlet, in usual state of preservation. *o.c*, outer cortex; *i.c*, inner cortex; *x*, xylem. × 16. S. Coll. 113. (G. T. G.)

(compare Fig. 97 with Fig. 101). The outer cortex answers to the raised external rim of the scar; the lacunar middle zone to its depressed surface; the inner cortex to the internal circle of the scar; and the vascular strand itself to the minute central point seen in the latter, when especially well preserved.

The rootlets of *Stigmaria ficoides* are absolutely the commonest specimens among the petrified material of

the calcareous nodules. Their structure is on the whole very uniform, though their dimensions vary greatly, the diameter ranging from a centimetre to a millimetre or less. The external cortex, which is generally well preserved, is several cells in thickness, and is often divided into an outer and inner zone by a band of thick-walled tissue. Sometimes the inner zone as a whole has thicker walls than the outer (Fig. 103), but often there is an entire absence of differentiation (Fig. 101). These distinctions may possibly turn out to be of specific value, but at present we have no clue to their significance. As we have already seen, all the layers of the cortex in the rootlet are continuous with the corresponding tissues of the main *Stigmaria*, and present similar characters. The outermost layer of the rootlet is sometimes papillose, but no true root-hairs have been observed.

Indications of tangential division are sometimes found in the cells of the external cortex, which may thus have undergone some slight secondary increase in thickness. Within this external zone we almost always find a wide empty space, from which all tissue has perished. It is rare, except at the base of the rootlet, to find any remains of the middle cortex, which must once have bridged the gap. Occasionally, however, especially in young rootlets, some thin-walled tissue is still preserved in this region, or a single, stout trabecula may connect the inner with the outer cortex (Fig. 103).

The internal cortex forms a ring, of very small size compared with the outer layer, and immediately encloses the vascular strand (Figs. 101-105). As, after the decay of the intermediate tissue, there was nothing to

keep the internal cortex in place, we seldom find it in its natural central position; usually it is more or less excentric. It consists of a few layers of delicate parenchyma; an endodermis has not yet been distinguished.

We now come to the vascular strand, which occupied

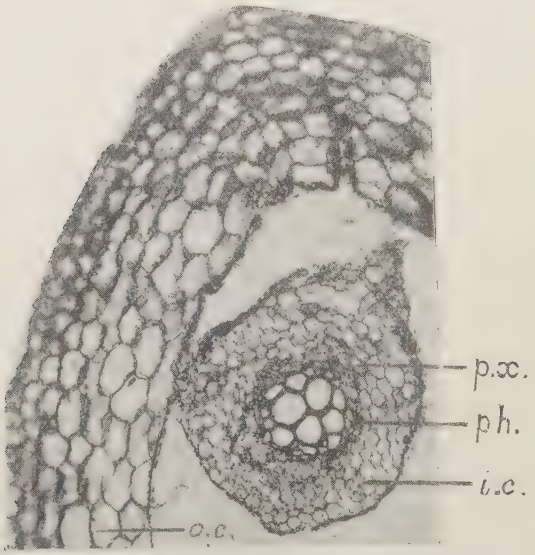

FIG. 102.—*Stigmaria ficoides*. Part of transverse section of rootlet, to show monarch structure. *px*, protoxylem, at one corner of the thick-walled strand of wood; *ph*, phloëm, which thins out opposite the protoxylem; *i.c*, inner cortex; *o.c*, part of outer cortex. × about 50. From a photograph by Dr. Bousfield. S. Coll. 114.

the central position in the whole structure. As a rule the wood only remains; occasionally, as in the specimen shown in Fig. 102, the delicate tissue which no doubt constituted the phloëm, and perhaps the pericycle also, is preserved. We will consider the xylem first. It consists of a small strand of tracheides with a somewhat triangular transverse section (Figs. 101-105). One

angle is more prominent than the others, and is in contact with the surrounding parenchyma (Figs. 102-104, *px*). At this angle the smallest elements are situated, and longitudinal sections show that they alone are spirally thickened; the remaining elements of the xylem are scalariform. It is therefore clear that the rootlet had only a single group of protoxylem, and thus, if we are to adopt the terminology usual in the case of roots, must be termed monarch. This conclusion is confirmed by the comparison of rootlets at various stages of growth, which always show the first differentiated tracheae at one angle only, never at three. So far as the English specimens are concerned, there can be no doubt that in *S. ficoides* all the appendages agree in having a monarch vascular strand.

A remarkable feature in the structure of the Stigmarian rootlet has recently been investigated by Professor F. E. Weiss.[1] Renault in 1882 had described rootlets with a very delicate vascular strand given off from the stele, and had regarded this as indicating a mode of branching distinct from the usual dichotomy. Professor Weiss confirms this observation (on which some doubt had been cast), but finds that the vascular strands in question have no connection with branches. They consist of spiral tracheides, and start from the protoxylem, pass out, obliquely or horizontally, through the middle cortex, enclosed in a sheath or traversing a trabecula, and terminate in connection with an extensive patch of tracheidal tissue in the outer cortex (Fig. 103).

[1] "On *Xenophyton radiculosum* and on a Stigmarian Rootlet," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. xlvi. 1902; "The Vascular Branches of Stigmarian Rootlets," *Ann. of Bot.* vol. xvi. 1902; "The Vascular Supply of Stigmarian Rootlets," *ibid.* vol. xviii. 1904.

On Professor Weiss's view "the vascular strand and the transfusion cells in which it terminates form a special means of conducting water from the peripheral to the central tissues of the rootlet, a means which is rendered necessary by the development of the middle cortex into an air-conducting tissue or space."

When the phloëm is preserved, it appears to be

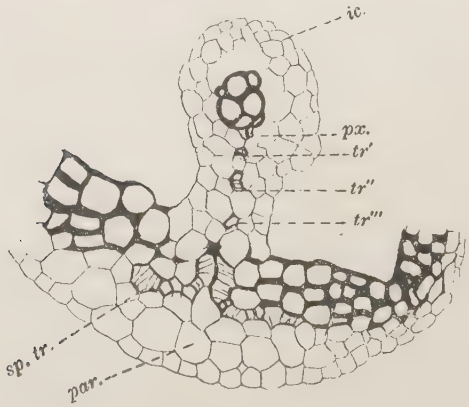

FIG. 103.—*Stigmaria ficoides*. Transverse section of rootlet, showing vascular bundle and part of cortex; *i.c*, inner cortex, connected by a parenchymatous bridge with the outer cortex; *px*, protoxylem; *tr'*, *tr''*, *tr'''*, three portions of vascular strands running to outer cortex; *sp. tr.*, spiral tracheides of outer cortex; *par.*, patch of large-celled parenchyma. × 67. After F. E. Weiss. Hick Collection (Manchester), 75.

thickest at the side remote from the protoxylem-angle, extending also along the flanks of the xylem, but not round the point (see Fig. 102, *ph*). It must be remembered, however, that in the state of preservation of these specimens the phloëm cannot be distinguished with certainty from pericycle or from cambium.

The elements of the wood do not, in the ordinary cases, show any radial arrangement, and are no doubt to be regarded as primary. In exceptional cases,

however, we find an addition of radially arranged secondary wood (see Fig. 104, x^2), and where this is the case the secondary formation is always limited to the side remote from the protoxylem, thus affording yet another indication of monarch structure. The formation of secondary wood, though rare in the free rootlets, is

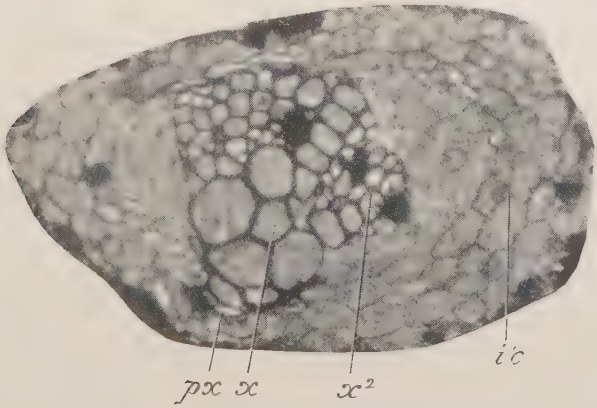

FIG. 104.—*Stigmaria ficoides.* Transverse section o central part of rootlet, to show secondary thickening of wood. *x*, primary xylem ; *px*, protoxylem ; x^2, secondary xylem, limited to one side of bundle ; *i.c*, inner cortex. × nearly 100. From a photograph by Mr. L. A. Boodle. Will. Coll. 651.

commonly found in the rootlet-trace, where it passes through the cortex of the main axis.

The branching of the rootlets was by dichotomy. A transverse section of a rootlet at the point of bifurcation is shown in Fig. 105. The plane of division passes through the protoxylem, and coincides with the plane of symmetry of the bundle. The dichotomous branching is an obvious point of agreement with the roots of modern Lycopods.

Something may now be said of other forms of

Stigmaria, differing in certain respects from the specimens grouped under *Stigmaria ficoides*.

Xenophyton radiculosum, a fossil described by Mr. T. Hick in 1891,[1] has been shown by Professor F. E. Weiss, in agreement with a suggestion of Williamson's, to be a *Stigmaria*. The pith and the whole of the cortex are preserved, giving the specimen a very different character from that of the ordinary *S. ficoides*. The wood,

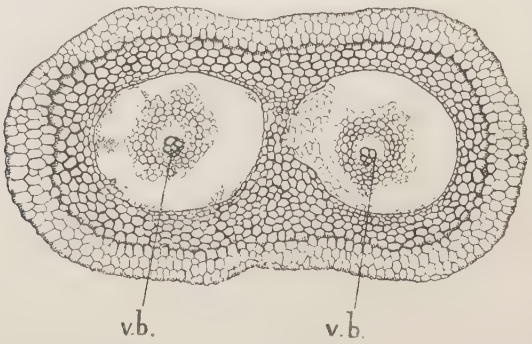

FIG. 105.—*Stigmaria ficoides*. Transverse section of rootlet, showing dichotomy. The outer cortex, differentiated into two zones, is still continuous, while the inner cortex of the two branches has completely divided. *v.b.*, the two monarch vascular bundles. × 25. S. Coll. 172. (G. T. G.)

which is little developed, appears to be wholly centrifugal, as in that species. The rootlet-bundles take a steeply acropetal course, like leaf-traces, and secondary parenchyma is formed about them in passing through the middle cortex, which has a similar structure to that of *Lepidophloios fuliginosus*, the plant to which Professor Weiss believes this *Stigmaria* to have belonged. Within the periderm there are strands of secretory cells, as in so many Lepidodendroid stems. It was in a

[1] Hick, "On a New Fossil Plant from the Lower Coal-measures," *Journal Linnean Society*, vol. xxix. 1892.

rootlet, attributed to the same plant, remarkable for the perfect preservation of the middle cortex, that Professor Weiss first observed the radial vascular strands, thus confirming Renault's previous statement.

As mentioned above, the absence of centripetal primary wood from the main axis is not constant in *Stigmaria*. M. Renault [1] found this tissue in various cases, and notably in a *Stigmaria* which he attributed to *Sigillaria Brardi*. Here the centripetal wood is very distinct, though of no great thickness. It forms more or less separate bundles, so that the structure is not unlike that of the corresponding part of the aërial stem.

Another species with centripetal wood, the *Stigmaria flexuosa* of Renault, is regarded by Solms-Laubach [2] as having very probably belonged to the fossil called *Stigmariopsis*, a form which differs in the shape of the scars from the ordinary *Stigmaria*, and which is characterised by its well-marked medullary casts, resembling those of a Calamite, though of course without the nodal constrictions. Solms-Laubach, from the geological distribution of *Stigmariopsis*, suggests that it may have constituted the underground organs of the *Sub-Sigillariae*, while the typical *Stigmariae* belonged to *Eu-Sigillariae* as well as to *Lepidodendron*. This, however, is not yet established, and, in fact, there are few questions in fossil botany more difficult than that of the relation of *Stigmaria* to its stems.

Professor F. E. Weiss has quite recently described a very interesting *Stigmaria*, from the nodules of the Lower Coal-measures, which possesses a perfectly

[1] *Flore fossile d'Autun et d'Epinac*, Part ii. p. 226, Plates xxxviii.-xl.
[2] *Ueber Stigmariopsis*, Jena, 1894.

distinct centripetal primary xylem, surrounded by a wide zone of secondary wood. This fossil was originally described by Williamson as an advanced condition of the stem of *Lepidodendron* (now *Bothrodendron*) *mundum*. It is probable that it really belongs to that plant,

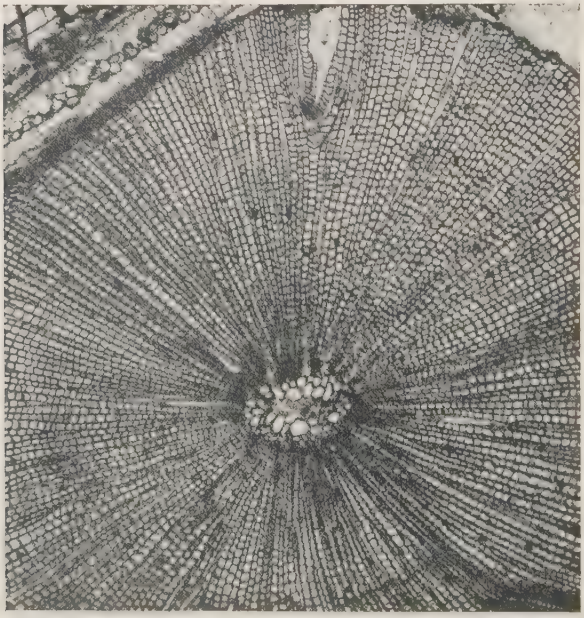

FIG. 106.—*Stigmaria*, sp. Transverse section of an axis, showing pith and large-celled centripetal primary xylem, with broad zone of secondary wood. At the top of the figure the bundle of a rootlet is seen. × 24. From a photograph lent by Professor F. E. Weiss.

representing its root or rhizophore. The primary wood gives the axis its stem-like character, but it is shown to be of the nature of a *Stigmaria* by the structure of the cortex and by the bases of rootlets attached to it. The rootlet-bundles are remarkable for having, usually, a mesarch xylem, with secondary growth on all sides,

instead of on the outer side only, as in *S. ficoides*. In passing through the cortex these bundles are connected with groups of reticulate tracheides, which probably served for water-storage.[1] If this *Stigmaria* is rightly attributed to *Bothrodendron mundum*, of which Mr. Watson has now described the cone, that plant will become the most completely known of the Palæozoic Lycopods.

3. *Morphology*.—It only remains to consider very briefly the morphological nature of *Stigmaria* and its appendages. If we call *Stigmaria* a "root," it is chiefly on physiological grounds that the term is used. The main axis of *Stigmaria ficoides* has in no respect the structure of a root; in fact, this species, in the absence of centripetal wood, departs from typical root-structure more widely even than the aërial stems themselves. Other forms of *Stigmaria*, though they may possess centripetal wood, are no more root-like in structure than the Sigillarian stem. The arrangement of the appendages (which, in the rare cases where the growing end is preserved, are found to have converged to form a kind of bud at the apex of the main Stigmarian axis) is unlike that of rootlets, nor does their origin seem to have been endogenous.

On the other hand, the appendages agree so exactly in structure and in the dichotomous mode of branching with the monarch roots of the allied recent genera *Isoëtes* and *Selaginella*,[2] that it seems impossible to

[1] Weiss, "A *Stigmaria* with Centripetal Wood," *Ann. Bot.* vol. xxii. 1908.

[2] In the Stigmarian appendages the position of the phloëm, which appears to have formed an arc on the side of the strand remote from the protoxylem, agrees exactly with that in the roots of these recent plants.

doubt their homology. Some authors have regarded the appendages as modified leaves, a view which was primarily suggested by their arrangement on the axis. Recent discoveries have tended somewhat to increase the analogies with leaves; the so-called transfusion-tissue of the Stigmarian rootlet (see above, p. 253) has been compared with that of the leaf, though the two tissues differ as much in arrangement as they no doubt did in function. Quite recently Professor Weiss has found, in connection with the rootlet-trace of the Stigmarian *Xenophyton*, a strand of cells analogous to the parichnos of the leaves, but situated on the opposite side of the bundle (next the xylem instead of next the phloëm).[1] Such resemblances as these do not count for much in establishing an homology, as Professor Weiss points out. On the other hand, the course of the rootlet-traces in *Xenophyton*, as already mentioned, is remarkably like that of the leaf-traces in the stems of Lepidodendreae.

The arguments in favour of the root-nature of the appendages are their dichotomous branching, monarch structure, general resemblance to the root of allied recent Lycopods, and the occurrence of secondary thickening. In favour of their homology with leaves we have their quincuncial arrangement (see Fig. 97), bud-like convergence at the apex, the transfusion-tissue

Cf. Bruchmann, *Selaginella spinulosa*, Plate i. Fig. 13, 1897; Farmer, "On *Isoëtes*," *Ann. Bot.* vol. v. Plate v. Fig. 4, 1891; Scott and Hill, "Structure of *Isoëtes Hystrix*," *Ann. Bot.* vol. xiv. Plate xxiv. Fig. 30, 1900. For information on the structure of rhizophore and root in many species of *Selaginella*, see Harvey Gibson, "Contributions towards a Knowledge of the Anatomy of the Genus *Selaginella*, Part iv. The Root," *Ann. Bot.* vol. xvi. 1902.

[1] Weiss, "The Parichnos in the Lepidodendraceae," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. li. 1907.

and parichnos, and the course of the rootlet-traces. There is no analogy among the Lycopodiales for such a modification of a leaf, but the water-leaves of *Salvinia* might be cited as remotely comparable. The presence of leaf-like characters in the Stigmarian appendages may be in part the survival of a more primitive morphology, but on the whole it seems evident that they are the same organs as the roots of recent Lycopods. Their apparently exogenous origin offers no hindrance to this interpretation, for we know that among recent Lycopods, as in *Selaginella* and *Phylloglossum*, roots may arise exogenously.[1]

What view, then, are we to take of the organs which bore the appendages? They are, as we have seen, often very different from typical roots. Neither, however, do they show the characters of rhizomes; they bear no leaves, and we have no convincing proof that they gave rise to aërial stems, though it is possible that they may have done so. Those *Stigmariae*, however, the relations of which are the most clear, are beyond doubt appendages of the aërial stems, and not their parent organs. How those stems arose in the first instance, whether directly from the embryo, or from some creeping form of axis, of which, as a rule, no traces remain,[2] is at present an unsolved problem.

It appears, then, that the main *Stigmariae* cannot be classed morphologically either as roots or rhizomes.

[1] Van Tiegham et Douliot, "Origines des membres Endogènes," *Ann. des sci. nat.* (*Bot.*), ser. vii. vol. viii. p. 552, 1888; Bower, "On the Development and Morphology of *Phylloglossum Drummondi*," *Phil. Trans.* ii. 1885.

[2] M. Grand'Eury maintains the latter view. See his *Bassin houiller du Gard*, p. 236; also "Sur les Sols de Végétation fossiles des Sigillaires et des Lepidodendrées," *Comptes Rendus*, t. cxxxviii. 1904.

The leafless rhizomes of *Psilotum* and *Tmesipteris* offer but a poor analogy, for they bear no roots or other appendages, except hairs. The best analogy we can find for the Stigmarian organs is in the rhizophores of *Selaginella*. These, like the former, are leafless branches, having no other function than to bear the roots; they may also be regarded as being themselves modified roots. In some cases, as we have seen above (p. 244), their structure shows some slight approximation to that of *Stigmaria ficoides*. The position of the rhizophores on the stem is, it is true, very different in the two genera, but this is not an insuperable difficulty, for we are not assuming a strict homology, but rather suggesting a parallel modification.

It may be suggested that the terminology most in harmony with the facts would be to call the main axis of *Stigmaria* a rhizophore, and its appendages roots. Considering, however, that even in existing Lycopods, as notably in *Lycopodium* itself, the differentiation between root and stem is often far less sharp than in other vascular plants,[1] we need feel no great scruple in applying the terms roots and rootlets to the Stigmarian organs, as was constantly done by Williamson, their chief investigator. Some further suggestions will be considered in Chapter XIV.

III. Lycopoditeae

Under this name are included certain fossil Lycopods, occurring from the Devonian onwards, which

[1] On this subject see C. E. Jones, "Morphology and Anatomy of the Stem of the Genus *Lycopodium*," *Trans. Linn. Soc.* ser. ii. vol. vii. 1905; G. Wigglesworth, "Young Sporophytes of *Lycopodium complanatum* and *L. clavatum*," *Ann. of Bot.* vol. xxi. 1907.

appear from their habit to have been herbaceous plants. One such herbaceous Lycopod—*Miadesmia*—has already been described in connection with its seed-like fructification (p. 197). As a rule, the Lycopoditeae are only known as impressions, but in favourable cases the essential morphological features can be recognised in these carbonised specimens. The plants, which until recently were all included in the genus *Lycopodites*, branched dichotomously, and have quite the habit of recent Lycopods; in some the leaves are uniform, as in most species of *Lycopodium*, while in others they are ranged in four rows, two of large and two of small leaves, just as in many species of *Selaginella*. This character is not, of course, sufficient in itself to establish affinity; within the last few years, however, the reproductive organs have been investigated in certain species and a clear relationship to *Selaginella* shown to exist. The genus *Selaginellites* has been founded by Zeiller for species known to have been heterosporous. *S. Suissei*, Zeiller,[1] from the Upper Coal-measures of Blanzy in France, has a dichotomous stem, with four rows of dimorphic leaves of the type of the tetrastichous Selaginellas. The strobili are of considerable size, 8-10 mm. in diameter by 15 cm. in length, with the sporophylls in numerous vertical series. The sporangia of the upper part of the cone contain numerous microspores, 40-60 μ in diameter, while those of the lower part are megasporangia, each of which contains from sixteen to twenty-four megaspores, about ten

[1] Zeiller, "Bassin houiller et permien de Blanzy et du Creusot," Fasc. ii., *Flore fossile*, 1906, p. 140. M. Zeiller's observations were first published in 1900.

times the diameter of the microspores (500-650 μ). Both kinds of spore have an equatorial ring or collar. The chief differences from *Selaginella* are in the numerous series of sporophylls, as compared with the tetrastichous vegetative leaves, and the relatively large number of megaspores in the sporangium, while in *Selaginella* they do not exceed four. M. Halle, in his recent paper on fossil herbaceous Lycopods,[1] describes a Coal-measure species (*S. elongatus* (Goldenberg)), likewise with dimorphic foliage, in which the sporangia appear to arise in the axils of ordinary leaves, no strobilus being differentiated. Microspores were not observed, but some of the sporangia were found to contain from twenty to thirty spores, about 450 μ in diameter, so there can be no doubt that the species was heterosporous; the absence of a specialised strobilus is interesting, as no such case is known among recent *Selaginellas*. Another species of similar age, investigated by M. Halle, *S. primaevus* (Goldenberg), is remarkable for its close agreement with the recent genus. In this case definite terminal strobili are differentiated; the sporophylls as well as the leaves of the smaller branches are uniform and spirally arranged (as in *Selaginella spinosa*), though it is possible that dimorphism may have occurred in the main stems. The most interesting point is that each megasporangium contained four tetrahedrally arranged megaspores (400-500 μ in diameter), just as in the living Selaginellas. Thus the *Selaginella* type, if not the actual genus, is shown to date from Palæozoic times. The species *S. Suissei* and

[1] Halle, "Einige krautartige Lycopodiaceen Paläozoischen und Mesozoischen Alters," *Arkiv för Botanik*, Stockholm, 1907.

S. elongatus may represent a less advanced condition, but it must be remembered that *Miadesmia*, a contemporary or older genus, went far beyond any other known herbaceous Lycopods in the specialisation of its megasporangia. Nothing certain is known, as yet, of any homosporous type of Lycopoditeae. If, however, the Rhaetic plant *Naiadita* is rightly referred to Lycopodiaceae, we may have an example from the Mesozoic, for the spores, which are found grouped in tetrads in the sporangia, have a diameter of 80 μ, and only one kind has been observed.[1]

Conclusion

We have now completed our survey of the Palæozoic Lycopods, a group remarkable for the high development which they attained, both in vegetative and reproductive characters. The anatomical complexity of the Lepidodendreae was clearly correlated with the arboreal habit, which was then so prevalent. Apart from this, the structure, so far as the primary tissues are concerned, was on the whole of a simple type—simpler than that of the majority of recent Lycopods. The remarkable morphology of the subterranean organs (*Stigmaria*) may possibly indicate a somewhat primitive stage in the differentiation of root and shoot, though it may also be interpreted as a special modification, due to the peculiar conditions of growth. The morphology of the vegetative organs, even in the highly organised Lepidodendreae, is not in itself

[1] See Miss J. B. J. Sollas, "*Naiadita lanceolata*," *Quart. Journ. Geol. Soc.* vol. lvii. 1901, p. 307.

inconsistent with the view that the Lycopods are among the most primitive of Vascular Plants.

On the other hand, the reproductive organs were generally of a very advanced type. With the still doubtful exception of *Spencerites*, it appears that all Palæozoic Lycopods of which the reproduction is known were heterosporous, and this applies, so far as our information extends, to the herbaceous as well as the arboreal forms. *Lepidocarpon* among the latter, and *Miadesmia* among the former attained, in the evolution of an organ closely analogous to a true seed, a higher level than any existing members of the Class, and rivalled the Spermophytes themselves.

Recent discoveries appear to show conclusively that *Selaginella*, at all events, had no direct connection with the Lepidodendreae, but sprang from a distinct and equally ancient herbaceous stock. If any modern member of the Class can claim affinity with the Tree Lycopods of the Palæozoic, it would appear to be the greatly reduced genus *Isoëtes*.[1] No light has yet been thrown on the ancestry of *Lycopodium*, which certainly had no near relation to any of the Palæozoic forms in which the nature of the spores has been determined.

In spite of the high organisation of the Palæozoic Lycopods, it is very doubtful whether they have any true affinity with the Seed-plants which some of them simulate, but this is a question which may best be postponed to the concluding chapter.

[1] See Chapter XIV.

CHAPTER VIII

THE FERNS

Fronds ; Fructifications ; Anatomy

We have now reached the fourth of the classes, or *phyla*, under which the Vascular Cryptogams—recent and fossil—naturally group themselves. This fourth phylum is that of the Filicales, or Ferns in the widest sense ; among all the Pteridophyta it is this stock which holds the strongest position at the present day. The Lycopods are unimportant now, compared with what they once were ; the Equisetales survive only in one single genus ; the Sphenophyllales disappeared altogether about the close of the Palæozoic period.[1] But the Ferns form one of the most prominent groups among living vegetation, numbering, on the most moderate computation, not less than 60 genera and 3000 species.

Until quite recently all palæobotanists held that the Ferns were even more important in Palæozoic times than they are at present, in fact that they were the dominant class of plants at that period. According to

[1] Unless we regard the Psilotaceae as their last surviving remnant ; see the concluding chapter of the book.

the estimates of the systematists the Ferns constituted almost exactly half of the total number of species known from the Carboniferous rocks. Now, however, the position has completely changed, so much so that Professor Zeiller, speaking of the Lower Carboniferous Flora, says that the Ferns, "though they were probably not entirely absent, occupied an altogether subordinate rank."[1] The ground for this radical change of view is to be found in the recognition of a new class of seed-bearing plants, the Pteridosperms, to which, as it now appears, the majority of the supposed Palæozoic Ferns really belonged. This class coincides in part with the Cycadofilices dealt with in the first edition of this book, but has proved to be much more extensive, and also more remote from the Ferns, than was realised at that time.

The reduction in the number of the true Ferns becomes more marked, the earlier the period to which we go back. "The Westphalian[2] Flora," according to Professor Zeiller, "is already less rich in true Ferns than the Stephanian,[3] and one might almost raise the question whether in the epochs of the Culm[4] and Devonian, Ferns really existed." The Pteridosperms, in fact, appear to be actually older than the majority of the known Ferns, though certain groups of the latter, such as the Botryopterideae, to be subsequently described, are doubtless of great antiquity.

From the characters of the frond alone (the part

[1] Zeiller, "Une nouvelle Classe de Gymnospermes: Les Ptéridospermes," *Rev. Générale des Sciences*, 16me année, 1905.

[2] Middle and Lower Coal-measures.

[3] Upper Coal-measures.

[4] Lower Carboniferous.

most commonly preserved) it is now impossible to say whether a given Palæozoic plant belonged to the true Ferns or to the Fern-like Seed-plants.

It is probable that the impressions of "Fern-fronds," often preserved in such exquisite beauty in the strata of the Coal-measures, are better known to the non-botanical observer than any other specimens of fossil plants. The character of such leaves has specially lent itself to this mode of preservation, and as regards form and venation, nothing more perfect could be desired than many of the impressions from the Carboniferous and other strata.

Almost all the well-known genera of conspicuous Fern-like fronds have now, however, fallen under suspicion. In several of them the presence of seeds has been actually demonstrated, in many others all the probabilities point the same way, but there is good reason to believe that some of these artificial form-genera include true Ferns as well as Seed-plants of similar habit. It will therefore be necessary, before going further, to say something of the fronds hitherto attributed to Ferns.

1. *Fronds.*—Brongniart was the first to construct a regular system of classification of the Fern-like plants, based entirely on the form and venation of the leaf, and since his time this system has been further elaborated, so that any fossil "Fern-frond" can now be referred to a provisional genus and species, according to its conformation and the course of its veins. The same system can be, and has been, applied to recent Ferns, and has, of course, proved to be purely artificial.

It would be quite useless for us to go into the distinctive characters of these provisional genera, which, while they are of the greatest use to those working practically at fossil floras, tell us nothing by themselves as to affinities. It will be sufficient to explain two or three of the principal generic names, which will frequently recur in our subsequent descriptions.

One of the largest of the artificial genera is that named by Brongniart *Pecopteris*, which includes many of the most striking Carboniferous "Fern-fronds," and is of special interest, because a good deal is known as to the fructification and anatomical structure of various plants which possessed this type of leaf. It is certain that some of its members were seed-bearing plants, but there is still a strong probability that others were true Ferns. The characters are thus given by M. Zeiller, whose diagnosis I have somewhat abridged :—"Fronds generally tripinnate, often quadripinnatifid or quadripinnate, more rarely bipinnate only. *Rachis of diverse orders naked between the pinnae*, or bearing pinnules between the latter. *Pinnules attached to the rachis by their whole breadth*, usually very broad, *contiguous*, sometimes more or less confluent, with parallel or slightly convergent margins, usually entire, more rarely lobed or dentate; apex usually obtuse, sometimes acute. *Median nerve distinct*, extending almost to the apex of the pinnule; *secondary nerves* pinnately arranged, *always springing from the median nerve, with which they make a wide angle, and not directly from the rachis;* sometimes simple, sometimes dichotomous."[1]

[1] *Bassin houiller et permien d'Autun et d'Épinac*, *Flore fossile*, Part i. 1890, p. 41.

The more essential characters are indicated by italics.

Among recent Ferns this form of frond is best represented among some of the Tree-ferns (Cyatheaceae). Fig. 107, illustrating the species *P.*(*Dactylotheca*)[1] *dentata*, will give a sufficient idea of the habit of a *Pecopteris* frond, though the true affinities of the plant are

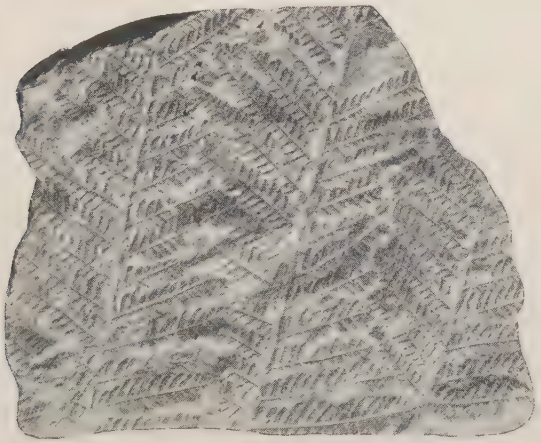

FIG. 107.—*Pecopteris* (*Dactylotheca*) *dentata*. Part of a frond, with the matrix. Reduced. From a photograph by Mr. W. Hemingway.

doubtful. There is good evidence that some of these fronds were really borne by Tree-ferns of the Carboniferous epoch, belonging, however, to a family quite distinct from that which includes our recent arborescent Ferns. A considerable variety of fructifications has been found in connection with fronds of the *Pecopteris* type; in many cases the reproductive characters point

[1] The second generic name, *Dactylotheca*, is based on the fructification, which happens to be known in this species. It may be Pteridospermous (see Fig. 109, C).

to an affinity with Marattiaceae, but in others they are of quite a different nature.

The important form-genus *Alethopteris*,[1] which comes near *Pecopteris* in foliar characters, is postponed to a future chapter, because there is reason to believe that all, or almost all, the species belonged to seed-bearing plants. The same remark applies to *Neuropteris*. We will therefore pass on to another of the great frond-genera, *Sphenopteris*, the characters of which are as follows :—"Fronds generally tripinnate or quadripinnate, more rarely bipinnate ; pinnules usually small, *contracted at the base*, with a more or less narrow pedicel, habitually divided into acute or rounded lobes, which are themselves contracted into a wedge towards their base. Nervules simple or branched, forming acute angles both with the median nerve and with their own branches."[2]

Generally speaking, the habit of the species of *Sphenopteris*, a most heterogeneous group, may be compared with that of members of the recent genus *Asplenium* (see Fig. 160, Chapter X.). The *Sphenopteris* type of frond is of great interest, not only on account of the elegance of its varied forms, but also from the fact that a great variety of fructifications, both Filicinean and Pteridospermous, have been referred to it.

The genus *Diplotmema*, Stur, as limited by Zeiller,[3] differs from *Sphenopteris*, only in the fact that the primary pinnae are forked, dividing into two similar branches, each of which is repeatedly subdivided, after the manner of *Sphenopteris*.

[1] See Chapter XI. Fig. 162.

[2] Zeiller, *l.c.* p. 30.

[3] *l.c.* p. 37.

In some species of *Sphenopteris* the main rachis is itself forked. These species, as well as *Diplotmema*, no doubt represent the foliage of Pteridosperms, but some other Sphenopterid fronds are known to have borne fructifications referable in all probability to Ferns (*e.g. Oligocarpia*, *Corynepteris*).

It will, of course, be understood that there are many other form-genera to which Fern-like fronds are referred by systematists; the enumeration of these would serve no purpose here. Full accounts of the artificial system of classification will be found in any of the manuals of fossil botany. Some other types of frond will be referred to in describing the Pteridosperms, for in the majority, as mentioned above, the evidence, either direct or indirect, indicates that the leaves in question belonged to seed-bearing plants. The well-known example of the recent *Stangeria*, which, when first discovered, was referred to the Fern-genus *Lomaria*, already showed plainly enough that Fern-like foliage is not necessarily any proof of close affinity with Filicineae.[1]

Before leaving the subject of the fossil Fern-like fronds, we may briefly mention the curious stipellar outgrowths, or adventitious pinnae, as they have been called, which occur on the rachis of many of these leaves, and are usually known as *Aphlebiae*. These bodies, when detached from the frond, have been described as independent genera of Ferns, or even as

[1] It is now generally admitted that there is a real relationship between the Cycadaceae (to which *Stangeria* belongs) and the Ferns, so that the occasional resemblance in the leaf-characters is not wholly without significance. The question is discussed at length in the following chapters.

Fucoid Algae, and when found *in situ* have sometimes been interpreted as epiphytic Hymenophyllaceae. There is, however, no longer any doubt that they formed part of the fronds on which they occur. The Aphlebiae are present in considerable numbers, along the rachis and its branches, in various forms of *Sphenopteris*, *Pecopteris*, *Neuropteris*, etc. They are common to fronds which were probably those of true Ferns, and to leaves which belonged to Pteridosperms. In some cases the Aphlebiae are entire, orbicular or spathulate, in others they are finely divided in a dichotomous or pinnate manner. They usually differ entirely in form from the normal pinnae of the frond to which they belong, but in some cases transitional conditions have been observed. The position of these organs shows that they are not directly comparable with the stipules of the Marattiaceae; the best analogy which has been suggested for them is with the feathery outgrowths which occur on the base of the rachis in the recent Cyatheaceous Fern *Hemitelia capensis*. In this case, as in that of the fossil forms, they were at one time described as independent parasitic Filmy Ferns.[1] M. Zeiller has pointed out that somewhat similar anomalous pinnae are also produced on the rachis of various species of *Gleichenia*, at the point where the frond resumes its growth after a period of rest.

2. *Fructifications.*—We will now endeavour to gain an idea of the nearer affinities of some of the fossils which there are still grounds for referring to the class

[1] See Schenk, "Palæophytologie" (in Zittel's *Handbuch der Palæontologie*, vol. ii. 1890), p. 141.

Filicales. The evidence from the fructification, when available, was formerly considered decisive, but we shall find that this is no longer necessarily the case (see p. 289); anatomical characters, if carefully interpreted, may carry equal weight.

A few of the chief forms of fructification attributed to Palæozoic Ferns will now be considered, in relation, where this is possible, to the form and structure of the fronds on which they were borne. Certain special groups, in which our knowledge of the plant as a whole is more complete than usual, will be dealt with later on (Chapter IX.).

In the majority of cases, fossil fructifications referable to Ferns have been found on specimens preserved as impressions. In favourable instances such specimens may show something of the structure, as well as the form of the reproductive bodies, for spores and the walls of sporangia usually have more or less cuticularised membranes, so that they withstand decay, and may often be found in a recognisable form in the carbonaceous layer coating the surface of the impression. In other cases, again, petrified fructifications have been found, and here, of course, the evidence as to structure is far more satisfactory, though the petrified specimens are usually fragmentary, and hence difficult to correlate with those in which the external characters are shown.

It has been customary, for some time past, to divide living Ferns into two main series—the Eusporangiatae and the Leptosporangiatae—according to the development of the sporangium, which arises from a group of cells in the former, and from a single cell in the

latter series. The distinction, though not so absolute as was at first supposed, coincides well enough with natural divisions, for the only two Eusporangiate families — the Marattiaceae and the Ophioglosseae—are very distinct from any of the Leptosporangiate groups.[1] In the living flora the latter enormously outnumber the former, as regards both genera and species. In dealing with fossil specimens it is, of course, impossible to study the development of the sporangium, and our judgment as to affinities must necessarily be based on the mature characters. The sporangia of the Marattiaceae and Ophioglosseae are, on the whole, of relatively large size, attached to the frond by a broad base, with a wall more than one cell thick, and without a definite annulus, though its place may be taken by a small group of thickened cells. In the former of the two families, we have also to consider the grouping of the sporangia, which are often united together in each sorus to form a synangium. Among the Palæozoic plants with a Fern-like fructification we find a surprisingly large proportion which present these characters, or some of them, and it was hence inferred, apparently with good reason, that in those early days the Eusporangiate section of Ferns, now so restricted, was predominant. It is especially the Marattiaceae to which this conclusion applied; the Ophioglosseae have not been determined, from the earlier strata, with any degree of certainty.

We will first consider a few representative fructifications of the Marattiaceous type, postponing the question whether they actually belonged to Ferns of that family

[1] See, however, Professor Bower's arrangement, given below, p. 352.

or not, and will begin with one in which very definite confluent synangia were present.

This fructification, to which the generic name of *Ptychocarpus*, Weiss, has been given, was borne on leaves of the *Pecopteris* form; the species described is *P. unitus*, Brongn., from the French Coal-measures.

The fructification of *Ptychocarpus unitus* was borne on the ordinary frond. The sporangia are grouped six to eight together, in circular sori; the sporangia of each sorus or synangium are united laterally among themselves, and are at the same time adherent to the central receptacle, which rises up in the middle of the group (see Fig. 108, C). The synangia are ranged in one or two series, along each side of the median nerve of the fertile segment (Fig. 108, A). They are prominent and shortly-stalked bodies (Fig. 108, B), which often became detached entire from the surface of the pinnule. As shown by the transverse section, each sporangium has a wall, or rather perhaps a tapetum, of its own, but the whole sorus is embedded in a delicate tissue, which is quite continuous round the periphery (Fig. 108, C). The receptacle is traversed by a vascular strand. The spores in each sporangium are numerous and very small, measuring only from 18 to 20 μ in diameter. There is no trace of an annulus. M. Renault, to whom our detailed knowledge of this fructification is due, conjectured, with much probability, that each sporangium discharged its spores through an apical pore. In general characters, the *Ptychocarpus* fructification approaches most nearly to that of the recent genus *Kaulfussia*, in which the synangia are also circular, but there are many

differences in detail. In *Kaulfussia* the interior of the synangium is hollowed out into a cup, into which the sporangia open, dehiscence taking place on the inner

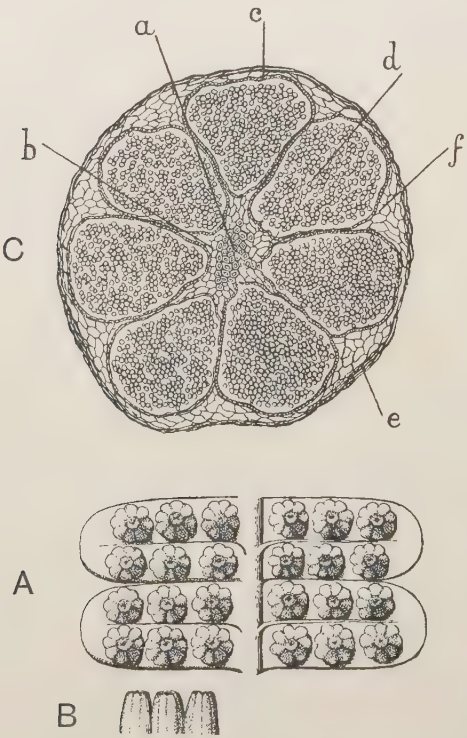

FIG. 108.—*Ptychocarpus unitus*. Fructification. A. Part of a fertile pinnule (lower surface), showing numerous synangia. B. Synangia in side-view. A and B × about 6. After Grand'Eury. C. A synangium, in section parallel to the surface of the leaf, showing seven confluent sporangia. *a*, bundle of receptacle; *b*, its parenchyma; *c* tapetum; *d*, spores; *e*, *f*, common envelope of synangium. × about 60. After Renault.

face of each sporangium. In the fossil genus there is no central depression, and, as the entire synangium was embedded in a continuous enveloping tissue, dehiscence could only have taken place at the apex.

The fructification of *Ptychocarpus unitus* is, however, a good example of a typical Marattiaceous synangium, and affords strong evidence as to the affinities of the plant.[1]

Mr. Watson has recently described, under the name *Cyathotrachus altus*, a synangium of Lower Coal-measure age, differing from *Ptychocarpus* in its taller shape, in having a cup-like central depression, and in the presence of tracheides at the base of the sporangia; in the two latter characters it approaches *Kaulfussia*. The specimens were isolated, but were associated with a pinnule, probably of a *Pecopteris*. There is a presumption in favour of Marattiaceous affinities, but the same doubts apply here as in other cases of the kind.[2]

The important genus *Asterotheca* resembles *Ptychocarpus*[3] in the fact that in each sorus the sporangia are grouped in a ring around the receptacle, but the receptacle is short, the sporangia are usually from three to six only in number, and are less closely united to one another. The sori are ranged on the under surface of the pinnule in two rows, one row on each side of the median nerve (see Fig. 109, A). The individual sporangia are ovoid in shape, and there is reason to believe that when ripe they separated from each other, bending outwards from the central receptacle, and dehiscing by a longitudinal opening on the inner

[1] See Renault, *Bassin houiller et permien d'Autun et d'Épinac*, Part ii. p. 9.

[2] D. M. S. Watson, "On a 'Fern' Synangium from the Lower Coal-measures of Shore, Lancashire," *Journal R. Microscop. Soc.* 1906, Part i.

[3] These genera are founded solely on the fructification, and are thus likely to represent more natural groups than those based on the form and venation of the frond. See Stur, "Zur Morphologie und Systematik der Culm- und Carbonfarne," *K. Akad. d. Wiss.* Vienna, 1883.

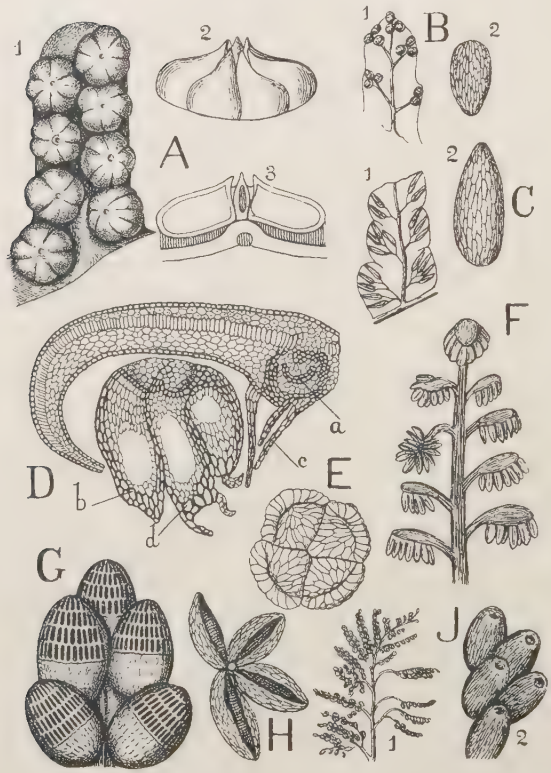

FIG. 109.—Group of Palæozoic fructifications of Ferns or Pteridosperms. A. *Asterotheca* (probably Marattiaceous). 1. Fertile pinnule showing eight synangia. Enlarged. 2. Synangium in side-view; 3. in section (diagrammatic). After Stur. B. *Renaultia*, Zeiller (affinities doubtful). 1. Pinnule, showing sporangia on veins. Nat. size. 2. Single sporangium. Enlarged. After Zeiller. C. *Dactylotheca* (affinities doubtful). 1. Pinnule, showing sporangia on veins. Nat. size. 2. Single sporangium. Enlarged. After Zeiller. D. *Sturiella*, Weiss (cf. *Corynepteris*). Transverse section of pinnule, showing a synangium. *a*, vascular bundle of pinnule; *c*, hairs; *b*, *d*, annulus of confluent sporangia. × 8. After Renault. E. *Oligocarpia* (cf. Gleicheniaceae). Sorus in surface-view. Magnified. After Stur. F. *Crossotheca* (♂ of Lyginodendreae). Fertile pinna, bearing several pinnules with sporangia. Enlarged. After Zeiller. G. *Senftenbergia* (cf. Schizaeaceae). Tip of fertile pinnule, showing five annulate sporangia. Magnified. After Renault. H. *Hawlea* (probably Marattiaceous). Synangium, after dehiscence of the sporangia. Magnified. After Stur. J. *Urnatopteris* (affinities doubtful). 1. Part of fertile pinna. Nat. size. 2. Sporangia, enlarged, showing apical pores. After Kidston.

side of each sac. Certainly some of the preparations show quite clearly that the sporangia are separate down to the base of the synangium. Forms with the sporangia distinctly separate are, however, regarded by Stur as constituting a different genus, to which he has given the name *Hawlea* (see Fig. 109, H). It thus appears that in *Asterotheca* and allied fructifications, the cohesion of the sporangia was much less perfect than in the living Marattiaceous genera *Kaulfussia*, *Danaea*, and *Marattia*.

A number of species with fronds of the *Pecopteris* type are known to have borne the fructifications of *Asterotheca*. They are chiefly characteristic of the Upper Coal-measures and Permian.

The genus *Grand'Eurya* of Stur is interesting from its resemblance to the recent *Angiopteris*. The fructifications in question were first described by Renault from silicified specimens, and referred by him to two species of *Pecopteris*, *P. oreopteridia* and *P. densifolia*.[1] The sporangia are inserted along either side of the *lateral* veins of the fertile pinnules, and appear to be quite free from each other. There is, however, some indication of a grouping of the sporangia in fours. Thus in *Grand'Eurya Renaulti* of Stur (attributed to *P. oreopteridia* by Renault) there are usually eight sporangia belonging to each lateral vein, and forming apparently two quadrate groups of four each. On account of the latter arrangement, Zeiller attributes these species to the genus *Asterotheca*; in *Grand'Eurya* there seems to be no formation of synangia, but Zeiller considers that this condition, as in *Hawlea*, is only due to age.

[1] Renault, *Cours de Bot. Fossile*, t. iii. 1883, p. 110, Plate 19.

Another genus, *Scolecopteris*, also belonging to *Pecopteris* according to its foliar characters, has the same arrangement as in *Asterotheca*, but the synangia are stalked, and the sporangia long and sharply pointed at the apex. Fructifications of *Scolecopteris* have been found in a silicified condition, and their structure has thus been more thoroughly investigated than is usually possible. In one species, *S. polymorpha*,[1] the large tripinnate fronds bear two long rows of sori on the lower surface of each pinnule. The sporangia in each sorus are four in number ; they are free for the greater part of their length, which reaches about 4 mm. ; at their base they are attached to the surface of the pinnule, and on their inner side to a short receptacle, not more than one-third as long as the sporangia (see Fig. 110). The receptacle is described by M. Renault as having a cruciform transverse section, each arm of the cross corresponding to one of the four sporangia constituting the synangium (see Fig. 110, A, *sp*). Each of the long, pointed sporangia has a wall with thickened cells on its free outer surface, but on the inner side the wall is thin. It is probable that this unequal thickness of the wall caused the dehiscence of the sporangium on the inner side, and thus worked in the same way as the annulus of ordinary Ferns. The margins of the pinnule were incurved, so as to partly cover in the sori. Another species of *Scolecopteris*, *S. elegans*, was investigated many years ago by Strasburger.[2] The sporangia are here smaller, and there are often five in each sorus. Towards the base they are confluent with one another,

[1] Renault, *l.c.* p. 116, Pl. 20, Figs. 1-10 (*Pecopteris polymorpha*).
[2] *Jenaer Zeitschrift für Naturwissenschaft*, vol. viii. 1874.

and with the central receptacle; higher up they become free, and dehiscence appears to have taken place on the inner side, where the sporangial wall was thinnest. Strasburger's remarks on the affinities of

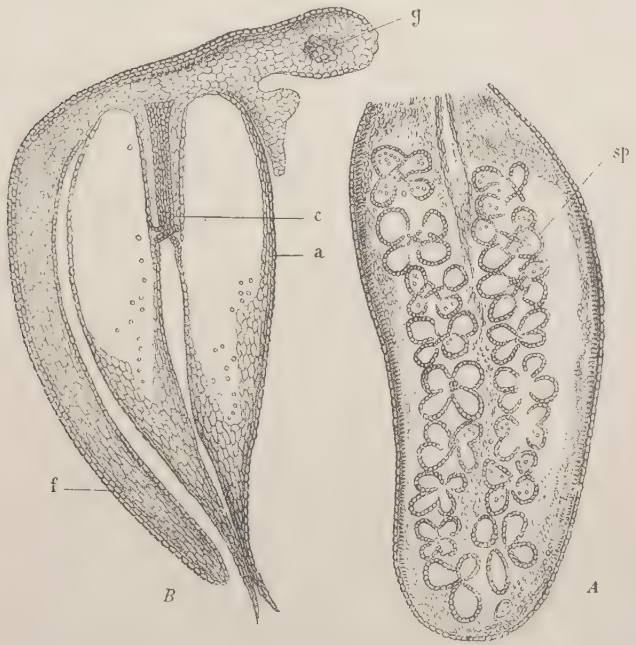

FIG. 110.—*Scolecopteris polymorpha.* A. Lower surface of a fertile pinnule, showing numerous quadrisporangiate synangia (*sp*). Note the cruciform receptacle at the centre of some of the synangia. × about 8. B. Transverse section of half a pinnule, passing through a synangium. *g*, vascular bundle of pinnule; *f*, infolded margin of pinnule; *a*, wall of sporangium; *c*, receptacle, fused to the sporangia. × about 18. After Renault.

this fossil may be quoted, for they apply to the genus as a whole, and express the view still generally held. "Zenker's *Scolecopteris elegans*, according to the formation of its sorus, certainly belongs to the Marattiaceae, and, in fact, comes nearest the genus *Marattia* in the

form of the sporangia of which the sori are composed, while it approaches the genus *Kaulfussia* in the circular grouping of the sporangia, and finally resembles the genus *Angiopteris* in the fact that the sporangia become free in their upper part. In the mode of dehiscence of the individual sporangia, *Scolecopteris* agrees with all three genera mentioned, but the similarity to *Marattia* is again the most striking, to which it also bears the greatest resemblance in the structure of the sori."

So far as the pedicellate sori are concerned, the agreement is especially close with the subgenus *Eupodium* of *Marattia*.

In the genus *Dactylotheca* of Zeiller, another of the *Pecopteris* group (see Fig. 109, C), the sporangia are somewhat similar in form to those of *Scolecopteris*. They are, however, completely independent of one another; each sporangium is placed singly over a lateral vein. The line of dehiscence can be recognised, but there is no trace of an annulus; it is mainly on this ground that *Dactylotheca* and various other genera with separate sporangia have been placed in the Marattiaceae. For example, in the genus *Renaultia* of Zeiller [1] (see Fig. 109, B), the ovoid sporangia are independent, isolated, or grouped in small numbers at the extremity of the nerves. In this case there is an indication of a rudimentary annulus, like that of the recent *Angiopteris*, at the apex of the sporangium. *Renaultia*, Zeill., was the fructification of certain species with fronds of the *Sphenopteris* type.

[1] *Hapalopteris* of Stur, whose genus *Renaultia* is quite different, having typical synangia. The nomenclature of these fructifications is lamentably involved.

It must be confessed that in such cases the reference to Marattiaceae has always rested on very slender evidence. Where no synangium is formed, and the sporangia are not even grouped in definite sori, we really have very little to go by, in default of anatomical evidence, for the mere absence or rudimentary development of the ring is of course no proof of Marattiaceous affinities. The position of genera such as *Dactylotheca* and *Renaultia* is entirely doubtful, and it is quite possible that their fructifications may really be of the nature of microsporangia, the plants being in that case Pteridosperms and not Ferns.

Among the Palæozoic plants with definite synangia, the circular or radiate type of synangium, now limited to the genus *Kaulfussia*, seems to have prevailed. In the genus *Danaeites*, however, which includes some Pecopteroid forms from the Coal-measures, the synangia were linear in shape, and appear to have closely resembled those of the recent genus *Danaea*. In this case the sporangia were arranged in a double row along each secondary nerve of the fertile pinnule; they were sunk in the tissue of the lamina, and fused laterally with one another, the constituent sporangia each dehiscing by an apical pore. The agreement with the recent genus was thus remarkably exact.

The forms hitherto described bore their sporangia on the ordinary vegetative fronds, as is the case with a majority of the Ferns at the present day. A considerable number, however, of the Palæozoic Fern-like plants were dimorphic, the sporangia appearing on fertile leaves, or parts of the leaf, quite different in form from the sterile foliage.

Many of these dimorphic fronds no doubt belonged to Pteridosperms and not to Ferns. Thus a species of *Crossotheca* (Fig. 109, F) has been shown by Mr. Kidston to be the male fructification of *Lyginodendron* (Chapter X.); *Calymmatotheca* is now known to represent a condition of the seed-bearing apparatus of the same genus; *Urnatopteris* (Fig. 109, J) is probably, like *Crossotheca*, a microsporangiate fructification. Some examples of dimorphic fronds in plants which appear really to come under the head of Ferns will be given in the next chapter in describing the Botryopterideae.

Before leaving the supposed Marattiaceous fructifications, we may shortly refer to a genus which combines Marattiaceous characters with those of other families. This is the *Sturiella* of Weiss (*Renaultia* of Stur). The structure of the leaf and sorus was worked out by Renault [1] from silicified specimens. The frond was of the *Pecopteris* type, though its form is not completely known, as the specimens were fragmentary. The sori are ranged in two series on the pinnule, along either side of its median nerve. Each sorus constitutes a synangium, for the five sporangia of which it consists are fused at the base, and attached by a short common pedicel to the lower surface of the pinnule (see Fig. 109, D). Hence their arrangement is altogether that of a Marattiaceous Fern. The structure, however, of the individual sporangia is peculiar, for the free end of each is capped by an apical annulus of large thick-walled

[1] *Cours de botanique fossile*, vol. iii. p. 122, 1883. M. Renault named the species *Pecopteris intermedia*. Stur appropriately founded the genus *Renaultia* for its reception, but this generic name was adopted slightly earlier by Zeiller for another fructification, above mentioned.

cells, which also extends for some distance along the outer side of the sac (Fig. 109, D, *b*, *d*). The annulus is accompanied by multicellular hairs.

The leaf was a thick fleshy one, with a layer of palisade-cells, but the most characteristic anatomical peculiarity is the horse-shoe bundle of the midrib (Fig. 109, D, *a*). Authorities differ as to the systematic position to be assigned to this curious Fern. Stur, relying on the characters of the sorus, places it among Marattiaceae, near *Asterotheca* and *Scolecopteris*, while Zeiller rejects this attribution, on account of the well-marked annulus. The latter feature suggests a comparison with Schizaeaceae or Osmundaceae, but Zeiller leaves the position of the genus an open question. On the whole, the balance of characters seems to weigh on the side of Marattiaceae, for there is no reason why the annulus, still represented at the present time in *Angiopteris*, should not have been more highly developed in some Palæozoic members of the family. A relation, through *Corynepteris*, to the Botryopterideae is also possible (see next chapter, pp. 323, 344).

This brings us to yet another genus, *Senftenbergia*, of still more dubious affinities. Several species have been included under this genus, the foliage of which was of the Pecopteroid type. The sporangia are inserted singly over the lateral nerves of the pinnules, near their outer end, so as to form a marginal series. There is thus no formation of synangia, or even of definite sori (see Fig. 109, G). In the typical species there is a definite apical annulus, several cells in width. *Pecopteris exigua*, referred to *Senftenbergia* by Stur, has no annulus, and appears to be a *Crossotheca* (see Chapter X.). The

sporangia of *Senftenbergia* find their nearest parallel in the Schizaeaceae, to which family Corda, the discoverer of the genus, referred it. The pluriseriate structure of the annulus has been brought forward as an argument against this view, but in *Lygodium*, among recent Schizaeaceae, the annulus, as Zeiller has pointed out, is often more than one cell in breadth.

Upon the data available, it remains impossible to determine the position of the genus. The analogy with *Angiopteris*, on which Stur, who maintained the Marattiaceous affinities of *Senftenbergia*, laid stress, appears remote. There is, however, some evidence that in the fossil genus the sporangial wall was several cells in thickness, a character which points in the direction of Marattiaceae.

Sporangial characters, like any other characters, are, in fact, insufficient *by themselves* to determine the position of a genus in a doubtful case.

The evidence for the Marattiaceous affinities of such genera as *Ptychocarpus*, *Asterotheca*, *Scolecopteris*, and *Danaeites*, in which the fructification is in the form of synangia borne on the ordinary foliage, is still generally accepted, and is much strengthened by the presence, at similar horizons, of stems (*Psaronius*) with a Marattiaceous anatomy (see below). Any doubt there may be arises from two considerations: (1) Practically all the fructifications in question were borne on *Pecopteris* fronds, and one species referred to *Pecopteris* (*P. Pluckeneti*) is now known to have been a seed-bearing plant (see Chapter XI.); (2) a species of *Crossotheca*, formerly regarded as a Marattiaceous genus, has been shown by Mr. Kidston to be the male fructification of the Pteri-

dosperm *Lyginodendron*, and the *Crossotheca* type occurs in species of *Pecopteris* (e.g. *P. exigua*) as well as in *Sphenopteris*. Even typical "Marattiaceous" synangia, such as those of *Scolecopteris*, are remarkably like other fructifications (*Telangium Scotti*, Benson) which there is reason to regard as microsporangia. Hence the question has arisen, whether all the supposed synangia of Marattiaceae may not represent the microsporangia of Pteridosperms, a suggestion which has been supported by the remarkably close agreement between the stamens of the Mesozoic Bennettiteae and the fertile fronds of Marattiaceae (see Chapter XIII.). On the whole, however, the balance of evidence, if we also take the anatomical data into account (see below, p. 294), is still decidedly in favour of the view that a considerable group of Marattiaceous Ferns existed in Carboniferous times, side by side with Pteridosperms of similar habit. The former are mainly, though not exclusively, characteristic of the Permian and Upper Coal-measures, and are not known to extend to the Lower Carboniferous.

As regards the other Eusporangiate family there is little to say. A couple of genera, *Rhacopteris* and *Noeggerathia*, formerly referred by Stur to the Ophioglosseae, were more probably the microsporophylls of Pteridosperms. A fructification resembling that of an *Ophioglossum* has been described by Renault, from the Permo-Carboniferous of Autun, under the name of *Ophioglossites*. We shall find in the Botryopterideae —to be described in the next chapter—a family, which, in certain characters, bears a resemblance to Ophioglosseae, though very different in other respects.

There is some slight evidence for the existence in

Palæozoic times of Ferns allied to Gleicheniaceae. As Professor Bower has pointed out, "the type of sorus" in *Gleichenia* "is that of the Marattiaceae."[1] Hence, on soral characters alone, it would not be possible to distinguish between a fossil fructification of this family and one of the Marattiaceae with free sporangia arranged circularly. The genus *Oligocarpia* of Göppert, with Sphenopteroid foliage, bore such sori, which in surface view certainly look wonderfully like those of a *Gleichenia* (see Fig. 109, E). Each sporangium shows a transverse, or somewhat oblique annulus, just as in that genus; though some authors have denied that the apparent annulus is really distinct from the rest of the sporangial wall, the inspection of the specimens, especially those of *O. robustior*, Stur, leaves no doubt that the former interpretation is correct. Zeiller, who supports the Gleicheniaceous affinities of this genus, further cites certain isolated sporangia, which have been found in the Quartz of Autun, as having unmistakably the characters of that family.

Sporangia with a transverse annulus, much like that of the Hymenophyllaceae, have been observed on the fronds of some Sphenopteroid Ferns from the Coal-measures (*Hymenophyllites quadridactylites*), but the evidence as to their position on the leaf is not sufficient to place the affinities of these fossils beyond doubt. The Devonian genus *Archaeopteris* or *Palaeopteris*, the type-species of which, the famous *A. hibernica*, is characteristic of the Old Red Sandstone of Ireland, was once referred by some authors to the Hymenophyllaceae, by

[1] "Studies in Morphology of Spore-producing Members," Part iv., *Phil. Trans. Roy. Soc.* vol. 192, B, p. 38, 1899.

others to the Marattiaceae, but is now regarded by Mr. Kidston as most probably a member of the Pteridospermeae.

The evidence for the existence of Palæozoic Osmundaceae is now under investigation;[1] it is not at all uncommon to find isolated sporangia in the petrified material, which might well be of that nature. The presence of a lateral group of enlarged cells, resembling the annulus or areola of Osmundaceae, is a frequent feature. Professor Bower some years ago drew attention to the Osmundaceous character of certain Carboniferous sporangia;[2] some of the sporangia of this type no doubt belonged to the Botryopterideae described in the next chapter.

In the calcareous specimens showing structure, from the British Carboniferous strata, sporangia like those of Ferns are frequent enough, but unfortunately they are usually isolated, so that it is impossible to tell what was their arrangement, or to determine the nature of the leaf on which they were borne. The specimens, however, prove the frequency, in Palæozoic times, of free sporangia not grouped into synangia. They also prove that the presence of an annulus of some kind was almost as common then as now, though the form of the annulus was, no doubt, different from that usual among recent Ferns. The generic name *Pteridotheca* may conveniently be used provisionally for such

[1] See the work of Kidston and Gwynne-Vaughan referred to below (pp. 345, 351).

[2] "Is the Eusporangiate or the Leptosporangiate the more Primitive Type in the Ferns?" *Annals of Botany*, vol. v. 1891. The *Sarcopteris Bertrandi* of Renault also has Osmundaceous characters (see *Cours de bot. foss.*, vol. iii. p. 129 Plate xxi. Figs. 12-15).

unassigned petrified sporangia, of Palæozoic age, as possess an annulus or other characters indicating Filicinean affinity. In Figs. 111 and 112, examples of Fern-sporangia from the English Coal-measures are represented. In the former figure two sporangia are shown, seated side by side on a fragment of leaf, in which a vascular bundle with scalariform tracheides is present. It will be noticed that the sporangia are free from each other, and that each shows a cap-like annulus, or group of enlarged cells, in the upper part. The fructification is certainly not a synangic one, but might conceivably belong to some Marattiaceous Fern comparable to *Angiopteris*, or might equally well be compared either with Schizaeaceae or Osmundaceae. An affinity with the Botryopterideae is, however, quite as probable (see next chapter). This fructification may be distinguished as *Pteridotheca Butterworthii*, after its discoverer.

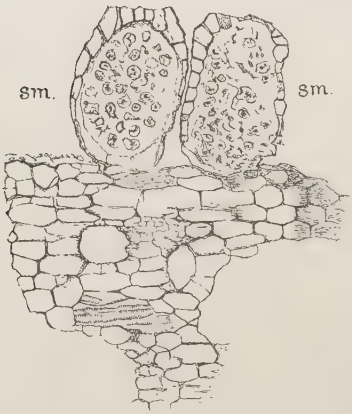

FIG. 111.—*Pteridotheca Butterworthii.* Fragment of a Fern-frond from the Coal-measures, in vertical section, showing two sporangia (*sm*), each with an apical annulus, and containing spores. In the tissue of the leaf, part of a vascular bundle is shown. × 34. Will. Coll. 1871. (G. T. G.)

In Fig. 112, on the other hand, we have a section passing through a large sorus, or rather a group of sori. The plane of the section was no doubt approximately parallel to that of the fertile frond, which was highly compound and apparently of the *Sphenopteris* type, the

lamina being well developed, like that of a vegetative frond rather than a specialised sporophyll. The pinnules are much incurved, and the sporangia are seated on their margins. In the section figured, several

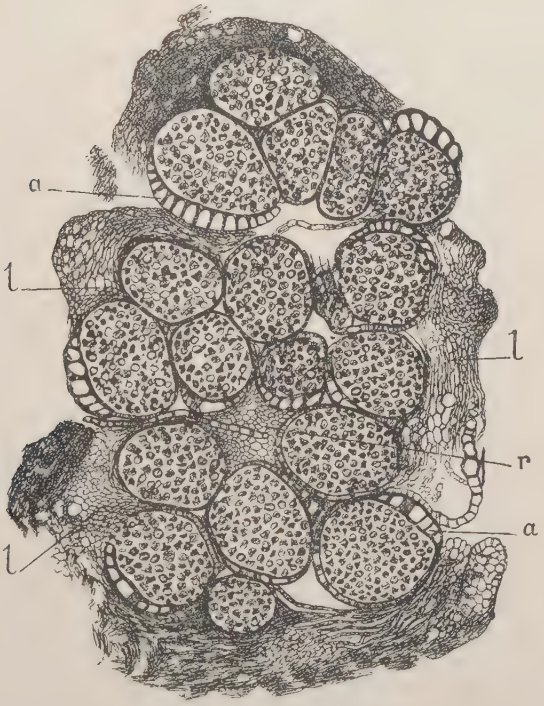

FIG. 112.—*Pteridotheca Williamsonii.* Group of annulate sporangia, seen in section, parallel to surface of frond. The sporangia contain numerous spores; at *a*, the annulus is specially clear. *l*, *l*, *r*, parts of tissue of the fertile pinnules. × 36. S. Coll. 215 (Coal-measures). (G. T. G.)

pinnules, cut in various planes, are shown. The sporangia are sessile, with a multicellular base, and are of nearly spherical form, except where their sides are flattened by mutual pressure. The most striking feature of the sporangia, which contain numerous small

spores, is the extreme distinctness of the annulus, which, when cut lengthways (*a*), quite suggests that of a Polypodiaceous Fern, and contrasts sharply with the small cells of which the remainder of the wall is composed. The annulus was evidently longitudinal or somewhat oblique, rather than transverse; it agrees in detailed structure with the annulus of recent Ferns, especially in the thinness of the external cell-walls, and the gradual thickening of the radial walls from without inwards; transverse sections of the annulus show, however, that it was regularly two cells in width, thus differing from that of any recent Ferns. Specimens of this fructification, which I have named *Pteridotheca Williamsonii*, are of frequent occurrence in the coal-balls of the Lower Coal-measures, and the preservation is often remarkably perfect. There is every reason to believe that it belongs to a true Fern, though it would be futile to seek for any near affinities with recent families.

Postponing any further discussion of the extent and character of the Palæozoic Fern-flora to the end of the following chapter, we will now pass on to consider some cases in which the anatomical structure is preserved, and affords evidence of Filiciaean affinities. We will first discuss an important group of stems in which the structure appears to be of a Marattiaceous type.

3. *Anatomy — Psaronius.* — Among the Fern-like remains from the Permo-carboniferous strata, and especially from their upper beds, specimens resembling Tree-ferns, in habit not altogether unlike those of the present day, are conspicuous. Some of these plants

were of great size, with a stem reaching, it is said, as much as 60 feet in height.

The arrangement of the leaves on these trunks showed more variety than exists among living Tree-ferns. Thus, in the genus *Megaphytum* of Artis, the tall, somewhat slender stem bore the fronds in two vertical series, as shown by the distichously arranged leaf-scars, which were of large size, having a transverse diameter of 8 or 10, and a height of 5 or 6 cm. There was thus a certain superficial and deceptive resemblance to large specimens of *Ulodendron*, with which the older authors sometimes confused these stems. This phyllotaxis is apparently unknown among arborescent or erect Fern-stems of the present age, though frequent in the case of prostrate rhizomes. In other Palæozoic Tree-ferns the leaves were ranged in four vertical rows, while in others, again, and these the most numerous, a spiral polystichous disposition prevailed, as in the arborescent Ferns of the present day. To guard against misconception, it may be well to say at once that the Palæozoic Tree-ferns only resembled those of the present day in general habit; their affinities doubtless lay in a direction quite remote from that of the Cyatheaceae.

The polystichous stems, in which the external surface, bearing the foliar scars, is shown, are known by the name of *Caulopteris*, while a separate generic name, *Ptychopteris*, is applied to stems in another state of preservation, in which the cortex has been stripped off and the vascular system exposed. Lastly, yet another genus had been founded for those stems of Tree-ferns which are preserved in a petrified condition, so as to retain their internal structure; the latter, whatever the

disposition of their leaves may have been, are embraced under the common name *Psaronius*. We have thus a curious example of palæontological nomenclature, for one and the same stem, according to its mode of preservation, may be placed in any one of the three "genera," *Caulopteris* (or *Megaphytum*, as the case may be), *Ptychopteris*, or *Psaronius*. If the foliage and fructification were taken into account, still other generic designations would come into requisition. Yet these anomalies are unavoidable, for it is rarely possible to identify the same species through its different states of fossilisation.

For our present purpose, the name *Psaronius* is the most suitable, as it is with the anatomical structure of the stem that we are specially concerned.

The specimens of *Psaronius*, which are characteristic fossils in the Permian beds of Saxony and Central France, were perhaps the earliest known of any fossil vegetable remains with structure preserved. They were quite familiar objects, even to the general public, in the eighteenth century, for, owing to the beauty of their surface when cut and polished, they became, for a time, favourite articles of ornament, under the name of "Staarsteine."[1] The markings, to which they owed their popularity, depend on their anatomical structure.

The genus contains a great number of described species, and though some may have merely a palæontological value, many no doubt represent real distinctions among the plants when living. The species from the Upper Coal-measures and Permian agree in having a

[1] "Starling-stones," from the speckled surface. The technical name *Psaronius* has the same origin.

highly complex polystelic organisation, comparable to that of the most highly differentiated Fern-stems of our own day. The structure of the *Psaronii* has been worked out in a most elaborate manner by Corda, Göppert, and Stenzel in Germany, and by Zeiller and Renault in France. A very full description, covering many species and forming a model of fossil anatomical investigation, is that given by M. Zeiller in the first volume of the magnificent work, so often referred to, on the fossil flora of Autun and Epinac.[1] M. Zeiller, discarding the somewhat complex methods of arrangement of earlier authors, classifies the members of the genus according to their phyllotaxis, ranging them in three groups—the Polystichi, with numerous vertical series of leaves; the Tetrastichi, with four such series; and the Distichi, with only two. The illustration in Fig. 113 is taken from one of the Tetrastichous division; this group is the least important of the three in number of species, but the form selected, *Psaronius brasiliensis*, Brongn., shows the anatomical structure with remarkable clearness. This fossil, as its name shows, came from Brazil, and, though its source is still uncertain, is probably of Permian age, like the majority of the European species.

The stem, as in all the *Psaronii*, is made up of two well-defined regions—a central portion, including the whole of the vascular system proper to the stem,

[1] Corda, *Beiträge zur Flora der Vorwelt*, Prague, 1845; Göppert, "Die fossile Flora der Permischen Formation," *Palaeontographica*, vol. xii. 1864; Stenzel, "Ueber die Staarsteine," *Nova Acta*, vol. xxiv. 1854; Zeiller, *Bassin houiller et permien d'Autun et d'Epinac*, vol. i. 1890; Rudolf, "Psaronien und Marattiaceen," *K. K. Akad. d. Wiss. Vienna*, 1905; Stenzel, "Die Psaronien," *Beitr. z. Paläont. u. Geol. Oesterreich-Ungarns*, 1906.

and a broad peripheral zone of cortex, traversed throughout by innumerable adventitious roots, seen in approximately transverse section in our figure. In this case the limit between the two regions is sharply defined, by an almost continuous band of sclerenchyma. The immense development of the peripheral zone of roots is a most characteristic feature of the genus *Psaronius*. Most authors have regarded the zone in which the roots are embedded as forming part of the cortex of the stem, as in the Marattiaceae, in which the adventitious roots arise near the apex of the stem, and grow down through the cortical tissues for a long distance before they become free.[1] There are two difficulties in applying this interpretation to *Psaronius*. The connection between the roots and the surrounding tissue is much more intimate here even than in Marattiaceae, and the root-zone is never traversed by the leaf-traces, as it should be if it belonged to the primary cortex. It has therefore been suggested that the embedding tissue in *Psaronius* may be formed by the compacted hairs of the roots themselves ; in many cases the filamentous character of the tissue lends support to this explanation. On the other hand, the evident continuity between the tissue in question and the true cortex appears decisive in favour of the older view. Stenzel's explanation that the embedding tissue is a secondary zone, developed *pari passu* with the growth of the roots after the leaves had fallen, appears the most probable, the radial arrangement of the elements, often observable, agreeing well with a secondary

[1] See the well-known longitudinal section of the stem of *Angiopteris evecta* in Sachs's Text-book and other manuals.

development. The question, however, deserves further investigation.

In the central region of the stem we see at once that the vascular system is remarkably complex, consisting of a great number of regularly disposed steles,

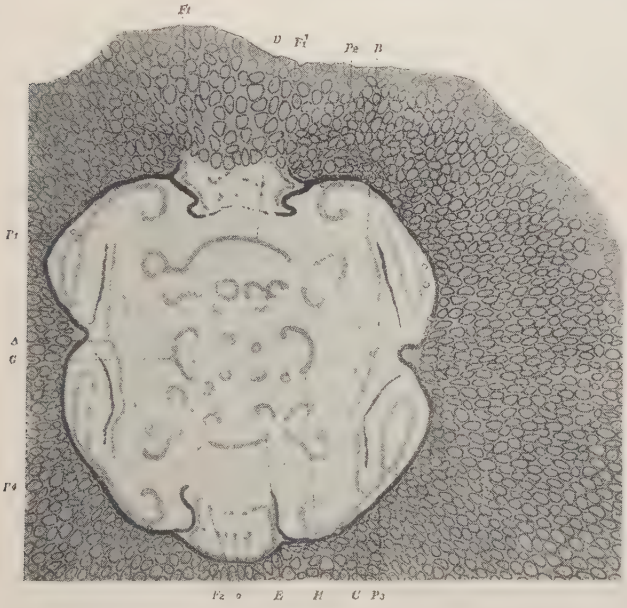

FIG. 113.—*Psaronius brasiliensis.* Transverse section of stem. The whole of the central portion, containing the vascular bundles, is shown, together with a great part of the cortex, traversed by innumerable adventitious roots. F1, F2, leaf-gaps. For detailed description, see text. The round objects at *o* are accidental perforations. Reduced. After Zeiller.

usually much elongated in transverse section, but varying greatly in size and form. At two opposite points (Fig. 113, F1 and F2) outgoing leaf-traces are shown. The leaves appear to have been decussately arranged, but those of the same pair were not precisely at the same level. At F2 the open curve of the out-

going stele is very evident; at F1, which is cut nearer its exit, the trace is apparently divided into two, and the sclerenchymatous zone has almost closed in behind it. Stenzel found, however, that the two arms of the leaf-trace always form part of a single horse-shoe or elliptical bundle.

A and B, at the sides of the figure, are the steles from which the leaf-traces of the next pair of leaves will be supplied, while D and E will give off, at a still higher level, the traces for the pair lying above F1 and F2. These four bands, corresponding in position to the four orthostichies of leaves, may be called the *reparatory* steles. At the four diagonal corners, we see four very long and curved steles (P1-P4), the "peripheral steles" of Zeiller, which have an important part to play. For one thing, it is from them that the adventitious roots take their rise; such roots are shown at several places between the peripheral steles and the sclerenchyma, or just passing through the latter. The peripheral steles are further concerned in the emission of the leaf-traces, for they anastomose with the reparatory steles immediately below the point where the leaf-trace passes out from the latter. Thus at C a branch is seen springing from the peripheral stele P3 to join the reparatory stele B.

The numerous internal steles—G, H, etc.—form a cauline system, the members of which, however, anastomose both among themselves and with the more external steles.

The whole subject of the vascular system of the *Psaronii* has been worked out by Zeiller, Stenzel, and Rudolf with a degree of completeness which could

hardly have been exceeded if they had been dealing with recent instead of with fossil plants. We have here only given the main results for this particular species, which, however, may serve very well as a type of the rest.

The more minute histology has also been worked out with a fair amount of detail. The steles have the typical concentric structure, each consisting of a band of wood surrounded by phloëm. The xylem is composed of scalariform tracheides with or without xylem-parenchyma, according to the species.

The ground-tissue is mostly parenchymatous, but internal sclerotic bands occur below the leaf-gaps (see Fig. 113, on the right and left).

The outer, radiciferous cortex consists of parenchyma, but each of the roots by which it is permeated is surrounded by a dense sclerenchymatous envelope, probably to be regarded as belonging to the root itself. In *Psaronius* generally, the structure of the roots is polyarch; in the particular species, *P. brasiliensis*, the number of xylem-angles is usually five or six. Phloëm and cortex are sometimes very fairly preserved, and in the latter, secretory sacs or canals are conspicuous. The roots strongly recall those of Marattiaceous Ferns now living.

A species, *P. Renaulti*, occurring in the roof-nodules of the Lower Coal-measures of Lancashire, is interesting from its exceptional antiquity and from the simplicity of its structure. The stem in this species contains a single annular stele, enclosing a large pith, and interrupted only at the exit of the leaf-traces, the sole instance, at present known, of a solenostele in a Palæo-

zoic stem. The phloëm, with its large sieve-tubes, is well shown in good specimens on both sides of the wood, and the protoxylem can be recognised, forming a number of small groups on the inner edge of the xylem, which is thus endarch (Fig. 114). Its position in the

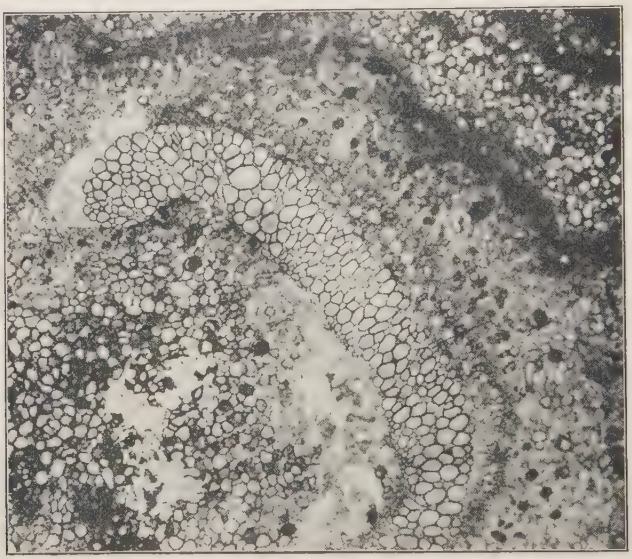

Fig. 114.—*Psaronius Renaulti.* Part of transverse section of stem, showing a portion of the solenostele. On the left is the edge of a leaf-gap. In the stele, note the protoxylem-groups on the inner edge of the wood. The phloëm, with large sieve-tubes, is well preserved on the outer side. The dark elements in the pericycle are secretory sacs. × 13. S. Coll. 2174. From a photograph by Mr. Tams.

numerous steles of the more complex species may be similar, but requires further investigation.

P. Renaulti may provisionally be regarded as the most primitive member of the genus. In a specimen probably referable to this species Mr. Butterworth made the interesting discovery that some of the roots show a

well-marked formation of secondary wood. A similar peculiarity has since been observed in a specimen of one of the Permian species. These are the only instances in which any trace of secondary tissues has been observed in the *Psaronii*, apart from the quite peculiar case of the radiciferous cortex.

The petioles of these Ferns have occasionally been found apart from the stems, and bear the generic name of *Stipitopteris*. They are identified by the comparison between their transverse section and the marks on the leaf-scars of the *Psaronii* in the *Caulopteris* condition. It appears that the petiole usually received a single large bundle with a horse-shoe section, the opening being on the upper side, with the free ends either strongly incurved, or replaced by a distinct strand, lying within the curve of the main bundle.

M. Grand'Eury, in his researches on the Coal-flora of the Loire,[1] found the stems of *Psaronius*, *in situ*, standing erect and rooted as they had grown. From the evidence of constant association, he has no doubt that their fronds were of the *Pecopteris* type, and identical with those on which fructifications such as *Asterotheca* and *Scolecopteris* were borne. This conclusion, which is confirmed by M. Renault's studies on the anatomy of certain *Pecopteris* leaves, would tend to show that the *Psaronii* were the stems of arborescent Marattiaceae, and there is little doubt that this was their true nature. There are, of course, various differences in detail, as, for example, in the great development of the sclerenchymatous tissues and in the single leaf-trace, points in which *Psaronius* diverges from the recent family.

[1] *Flore carbonifère du Département de la Loire*, 1878, pp. 78-98.

The recent work of Rudolf on the anatomical relations between *Psaronius* and the Marattiaceae has on the whole confirmed the long-established view of their affinity ; the common characters are to be found chiefly in the course of the vascular strands and in the structure of the roots, to which, as it now appears, the endarchy of the steles in the stem may be added. The evidence afforded by the *Psaronius* stems, taken in conjunction with that derived from the synangic fructifications, seems to leave little room for doubt that true Ferns with Marattiaceous affinities formed an important constituent of the Permo-carboniferous Flora, especially towards the close of that period. Where anatomical evidence is not available, it is, however, extremely difficult to distinguish between true Ferns of this group and plants more probably belonging to the Pteridospermeae.

CHAPTER IX

THE FERNS—*continued*

The Botryopterideae—Summary on the Ferns

I. BOTRYOPTERIDEAE

AMONG fossil plants generally, and in particular among those which may still be regarded as Ferns, it is only in rare cases that we are able to describe a plant as a whole, giving a connected account of all its organs. Where the evidence is such as to allow of even an approach to this desirable end, the fossil-botanist must regard himself as peculiarly fortunate.

For this reason the family of the Botryopterideae has long claimed a special interest among Palæozoic Filicales, for in two genera of this family the structure of all the important organs is fairly well known, and we have good evidence for connecting them together. Within the last few years the interest in this group has been greatly enhanced owing to the importance which now attaches to authentic Palæozoic representatives of the class of Ferns, and especially to such representatives as appear to have a primitive character.

The group, as we shall see presently, was in all probability an extensive one in Palæozoic times, but we will give our chief attention to those genera in which there is evidence as to the reproductive as well as the vegetative organs.

A. Zygopteris Group

1. *Zygopteris.* — We will first take the genus *Zygopteris*, founded by Corda in 1845, on a species described by Sprengel and Cotta a good many years earlier. A number of species have now been recorded, but in many of them the structure of the petiole only is known; our knowledge of the stem extends to four species: *Z. Brongniarti*, Ren.,[1] from the Permian of Autun, in France; *Z. scandens*, Stenz.,[2] from a similar horizon in Bohemia and Saxony; *Z. Grayi* (Will.),[3] and *Z. corrugata* (Will.),[4] from the Lower Coal-measures of England. *Z. scandens* and *Z. Grayi* were regarded by Williamson, in spite of the difference in geological age, as identical. The anatomical description will be based chiefly on *Z. Grayi*, which may best serve as the type of the genus. We shall find that, throughout this family, our knowledge is for the most part based on petrified specimens, so that while the anatomical data are full and fairly satisfactory,

[1] Renault, *Cours de botanique fossile*, vol. iii. chap. viii. 1883; for his original memoirs see *Ann. des sci. nat.* (*Bot.*), ser. vi. vols. i. and iii. 1875-76.

[2] Stenzel, "Die Gattung *Tubicaulis*," Cotta; *Bibliotheca Botanica*, Cassel, 1889.

[3] Williamson, "Organisation of Fossil Plants of Coal-measures," Part xv. *Phil. Trans.* 1889, B.

[4] Williamson, *op. cit.* Part viii. *Phil. Trans.* vol. 167, 1877.

the evidence as to external habit is comparatively scanty.

The stem of *Zygopteris Grayi* was from 10 to 15 mm. in diameter, and no doubt attained a considerable length. In fact, Stenzel regarded his closely similar form as a climbing plant, and hence named it *Z. scandens*, for he always found the stems and petioles of his specimens intermixed with the crowded roots of a *Psaronius*, among which he believes it to have scrambled, much in the same way as a *Tmesipteris* lives among the aërial roots of the New Zealand Tree-ferns at the present day. From the stem large petioles (little inferior to the stem in diameter) were given off, at considerable intervals; the phyllotaxis was a spiral one, and in certain cases, at any rate, the arrangement was clearly on the $\frac{2}{5}$ system (see Figs. 115 and 116).

In all the known Botryopterideae the stem was traversed by a single vascular cylinder; this monostelic structure, exceptional among recent Ferns, appears to have been more widely prevalent among those of Palæozoic age.

In our *Zygopteris* the stele has a very characteristic structure; its general form follows that of the wood, which in section has the outline of an irregular five-rayed star (see Figs. 115 and 116). These rays are of very unequal length; the comparison of successive transverse sections shows that the shortest are those which have just given off a leaf-trace (Fig. 116, 1), while the longest are those which are just about to do so (Fig. 116, 5). From the position of the leaf-traces and their relation to the prominent corners of the

wood, as shown in successive transverse sections, it follows that the angle of divergence between two successive leaves was in this case $\frac{2}{5}$ (Fig. 116, 1-5). A short xylem-arm from which the leaf-trace has just separated appears merely as a slight bulge (Fig. 116, 1);

FIG. 115—*Zygopteris Grayi*. Transverse section of stem, with axillary shoot and part of petiole. In the middle of the stem the five-angled stele is seen (cf. Fig. 116). *l.t.*, leaf-trace, about to give off the axillary strand; *s.l.*, "scale-leaf"; *ax.*, axillary shoot of next node below; *pet.*, part of petiole of the subtending leaf. The small strand in the cortex to the right belongs to a scale-leaf. × about 4. From a photograph by Mr. L. A. Boodle. Will. Coll. 1919 A.

those of successively greater length assume a truncated form at the end (Fig. 116, 2, 3, and 4); while the longest arms of all spread out laterally, so as to be broadest at their termination, acquiring a bicornute outline (Fig. 116, 5). It is the enlarged end of the arm which, at a somewhat higher level, becomes detached, to

form the xylem of a foliar bundle (Fig. 115, *l.t.*). In the wood of the stele, a central and a peripheral region may be distinguished. The peripheral tissue consists principally of large scalariform tracheides. Towards the ends of the more projecting arms, and especially at

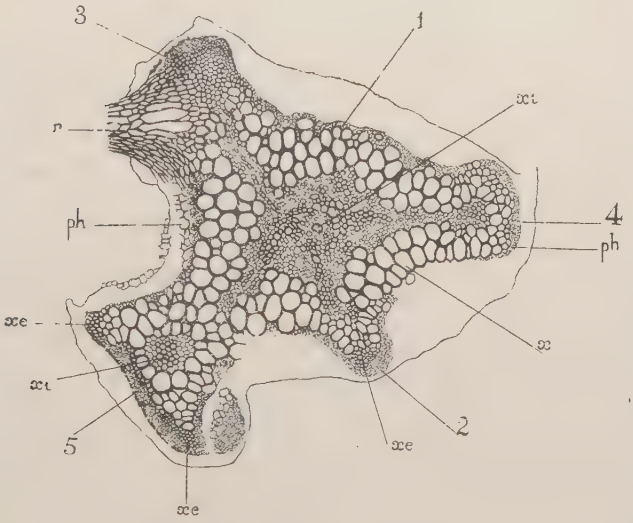

FIG. 116.—*Zygopteris Grayi.* Transverse section of stele, showing wood and remains of phloëm. 1-5, the five angles of the wood, from which leaf-traces are given off, in order of the phyllotaxis, No. 5 belonging to the lowest leaf of the series; *x* principal ring of xylem; *xi*, small tracheides of internal xylem; *xe*, small tracheides at periphery; *ph*, phloëm; *r*, base of adventitious root. × 14. Will. Coll. 1919 B. (G. T. G.)

the angles of the most prominent of them, much smaller elements occur (Fig. 116, *xe*). The central tissue, like the wood as a whole, has a stellate form; the main mass, which occupies the middle of the stele, sends out prolongations into each of the arms. The central tissue used at one time to be described as a pith, but that is not its true nature, for in addition to the delicate

parenchyma, it contains a system of small tracheides, quite distinct from those of the external xylem (Fig. 116, *xi*). This internal tracheal system forms a group or irregular ring about the centre of the stele, and from this central group radial bands of small tracheae extend outwards, up the middle of each arm (Fig. 116). The groups of small external tracheides (*xe* in Fig. 116) were no doubt continuous with the protoxylem of the foliar bundle, but they were also continuous, in the downward direction, with the smallest internal tracheides of the xylem-arms (see Fig. 116, at 2, which, however, is not cut quite at the right level to show continuity). Hence the transverse section shows both internal and external protoxylem.

Some remains of the phloëm which surrounded the wood of the stele are preserved; it includes a single or double series of large elements, which probably represent the sieve-tubes (Fig. 116, *ph*). The phloëm evidently followed the contour of the wood. The whole is surrounded by a zone of delicate tissue (which may best be regarded as an inner cortex), filling the spaces between the arms of the stele, and cylindrical in form (Fig. 116). Beyond this is the wide outer cortex, the internal layers of which are thick-walled, forming a kind of sheath to the inner cortical zone. The epidermis was provided with multicellular hairs.

The course of the leaf-trace bundles can be very clearly followed; a single large bundle entered each petiole. To form the trace the whole distal part of one of the prominent arms (cf. Fig. 116, 5) became detached, forming an approximately triangular concentric bundle, with the base directed outwards. In

this region the central tissue of the trace contains small tracheides, continuous with the internal tracheal group of the stele. At the two external angles are the groups of small elements which no doubt constitute the protoxylem of the foliar bundle.

As we follow the leaf-trace outwards through the cortex, we find that it divides into two strands, of very different form, both lying on the same radius (see Fig. 115, *l.t.*, where this division is just beginning). The outer of the two strands is the foliar bundle, which is continuous with the external side of the original triangular strand, while the inner strand is destined for the axillary shoot. We will first follow the course of the foliar bundle, which, as it separates from the inner strand and passes out into the petiole, gradually assumes a somewhat complex form. At first the bundle consists simply of a tangential, somewhat bent, plate of wood, surrounded by phloëm, and spreading out a little at either extremity, but in its outward progress these lateral expansions increase in importance, so that the ultimate form, in transverse section, is that of the letter "H," the cross-stroke of the H being placed tangentially with reference to the parent stem (cf. Fig. 118, from another species). The largest tracheides are in this middle band; the smallest, constituting the spiral protoxylem, are at the outer edge of the side-pieces. The phloëm surrounds the xylem and follows its contour. This H-shaped petiolar bundle is common, with slight modifications, to all species of *Zygopteris*, and, in fact, constitutes the character on which the genus was founded.

The other bundle, which is given off on the inner

side of the leaf-trace, between the latter and the stele of the stem, is of special interest. It is continuous with the adaxial part of the original leaf-trace, and as it separates, assumes an elliptical form in transverse section (see Fig. 115, *ax*), with the long axis placed tangentially. It consists of a ring of xylem, with large tracheides, surrounded by a zone of phloëm, and at the centre is a group of small tracheides accompanied by parenchyma. In fact, the structure of this bundle is that of the stele of the main stem, in an extremely simplified form. The *axillary strand*, as it is best termed, passed out into a cylindrical appendage, placed exactly in the axil between stem and leaf, and hence appropriately named by Stenzel the *axillary shoot* (Fig. 115, *ax*). This curious organ occurs in three out of the four forms of *Zygopteris* in which the stem is known,[1] but has not, so far as I am aware, been found in any other genus of fossil Ferns. There is, however, the closest possible analogy with the axillary branches of the recent Hymenophyllaceae, a family with which, in various other respects also, the Botryopterideae have much in common. Stenzel, the discoverer of the axillary shoots of *Zygopteris*, at first suggested another possible view of their nature, namely, that they might represent the fertile ventral lobe of the leaf, as in the Ophioglosseae. This was, at the time, a sufficiently probable interpretation, but was subsequently withdrawn by the author, on the ground that transitional forms occur, which are intermediate in structure between the

[1] The bundle marked *r* in Renault's figure (*Flore fossile d'Autun et d'Epinac*, Part ii. Plate xxxi. Fig. 2) of *Z. Brongniarti*, from its form and position, manifestly belongs, as Stenzel detected, to the axillary shoot, though interpreted by the author as an adventitious root.

axillary shoot and the normal stem of *Zygopteris*; this fact, which is also shown in the English specimens, seems quite conclusive in favour of the cauline nature of the axillary organ.

Besides the foliage-leaves, *Zygopteris* possessed rudimentary leaf-like organs, of small size, termed

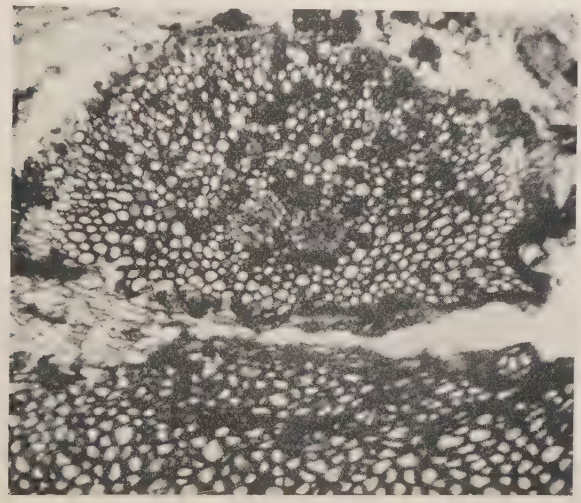

Fig. 117.—*Zygopteris corrugata*.—Transverse section of an "Aphlebia" with part of the outer cortex of the leaf-base to which it belongs. The appendage contains two vascular bundles. From a photograph by Mr. L. A. Boodle. × 36. Will. Coll. 264.

scale-leaves by Renault and Stenzel, who discovered them in *Z. Brongniarti* and *Z. scandens* respectively. I have recently observed them in the British species, *Z. Grayi* (Fig. 115) and *Z. corrugata* (Fig. 117), and am thus able to confirm the statements of the authors cited, as to which I previously felt some doubt. A curious feature of these appendages, which have a simple, scale-like form, is that they occur on the petiole-bases as

well as on the stem. A single bundle enters each appendage, and then divides into two, three, or four strands. An example from *Z. corrugata* is shown, in transverse section, in Fig. 117; it has just detached itself from the base of a petiole, and contains two bundles. The morphology of these curious organs, which in some respects recall the Aphlebiae of other Palæozoic Ferns and Pteridosperms, requires further elucidation.

The stem also bore adventitious roots; the vascular strands supplying them can be distinguished from those of the scales by their more horizontal course.

Such evidence as we possess from other species as to the form of the foliage-leaf will best be considered at a later stage, after the fructifications have been dealt with. The petiolar structure is better shown in some other forms of *Zygopteris*, the stems of which are not in all cases known. Thus in a petiole named *Z. Lacattii* by M. Renault, which is frequent in the English Coal-measures, as well as in those of France, all the tissues are sometimes well preserved. In this case the tracheides are generally pitted rather than scalariform, a character which was clearly very variable in this group, though of considerable constancy in other families. The subject of the so-called tracheides of Palæozoic Ferns and allied groups requires further investigation in the light of Mr. Gwynne-Vaughan's remarkable discovery that the scalariform elements of Ferns are not tracheides, but a peculiar form of vessel, in which not only the closing membranes of the pits, but the middle lamellae of the cell-walls are absorbed, leaving only the bars of thickening, connected by the

solid vertical angles of the vessels. This unexpected result, which was first suggested by observations on fossil Osmundaceae, goes to show that the true scalariform duct, far from being primitive, is a highly modified form of tracheal organ.

The protoxylem in *Z. Lacattii* occurs, as already mentioned, on the outside of the two lateral bands of wood, forming two groups on each side. The phloëm surrounds the wood completely, and contains large elements, presumably the sieve-tubes; the whole bundle is enveloped by a dense sheath. The inner parenchymatous zone of the cortex is traversed by numerous sacs, supposed to have been of a secretory nature. The outer layers of the cortex form a continuous zone of thick-walled mechanical tissue.

The leaf was obviously a compound one, for lateral bundles are given off from the side-pieces of the main strand, starting from the points where the spiral elements are placed. There were thus four rows of appendicular bundles in all, two on each side of the petiole. The significance of this peculiar arrangement, which was widely distributed in this family, is not yet understood In some cases there is evidence that the smaller lateral strands supplied the "Aphlebiae," but in other cases they certainly passed into branches of the rachis. Mr. Tansley,[1] on theoretical grounds, suggests that "this tendency to radial organisation of the frond may perhaps be regarded as a relic of the time when the structure of the fronds of Ferns was but little differentiated from that of the stem."[1] It must be

[1] "I. Lectures on the Evolution of the Filicinean Vascular System. II. The Botryopterideae," *New Phytologist*, vol. vi. 1907, p. 65.

remembered, however, that in these Botryopterideae we are often dealing with specialised fertile fronds.

Our illustration (Fig. 118) is taken from the petiole of another species, *Z. bibractensis*, Ren., in which the structure is rather more complex. The bundle has essentially the usual H-like sectional form, but

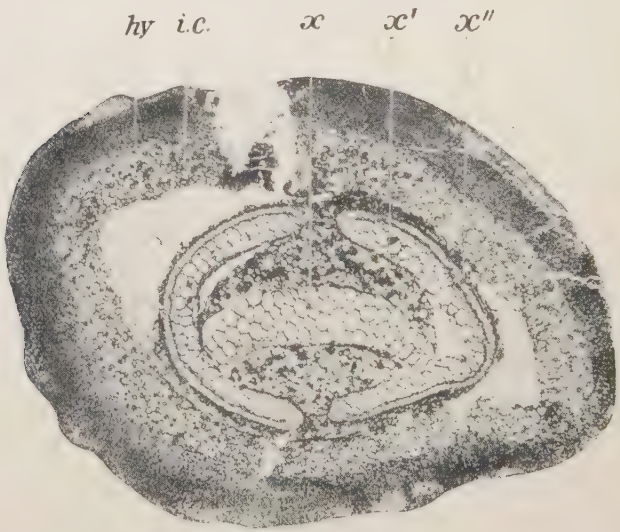

FIG. 118.—*Zygopteris bibractensis*. Transverse section of a petiole, showing the double-anchor form of stele. *x*, middle band of xylem; *x'*, the main lateral bands; *x''*, the small-celled external arcs of xylem; the protoxylem lies between *x'* and *x''*; *i.c.*, inner cortex; *hy*, sclerenchymatous hypoderma. × 7. From a photograph by Mr. L. A. Boodle. S. Coll. 914.

the lateral pieces are considerably incurved, giving to the whole the shape of a double anchor. The peculiar feature of this species consists in the presence of an additional external band of xylem (*x''*) on the outer side of each of the lateral plates (*x'*), separated by parenchyma from the main lateral plate, but united with it at its two ends (Fig. 118). The external bands

consist of smaller elements than the rest of the wood; the spiral tracheides are placed on the inner edge of the external bands. It was from the latter that the strands were given off, which passed out into the leaflets. In this species we find once more that the scalariform type of tracheides prevailed. The petiole bears characteristic spines, formed of sclerotic tissue.[1]

In connection with the petiole just described, a few words may be said about *Z. corrugata* (Will.),[2] a species in which all the vegetative organs are known. The petiole (once called *Rachiopteris insignis*, but already identified by Williamson) has the complex "Bibractensis" type of structure. The stele of the stem has an almost cylindrical form, except where it is affected by the emission of a leaf-trace, which is preceded by the formation of a double lobe, quite comparable to a bicornute arm of the stele in *Z. Grayi*. The system of internal tracheides is the same as in that plant, but in *Z. corrugata* there is no external protoxylem; its absence is correlated with the fact that the protoxylem-groups of the leaf-trace are immersed, as continues to be the case when the petiolar strand assumes its ultimate structure (cf. *Z. bibractensis*). The leaf-trace,

[1] It must be remembered that, in the case of these isolated petioles, the affinity with the more complete specimens of *Zygopteris* is not strictly proved, for we have only the anatomical characters of the petiole to judge by. These characters, however, are so peculiar that we run no risk of serious error in taking them as a provisional guide to affinity. In any case the question is not a very grave one, for we know enough of the petioles actually connected with the stem in other species, to be certain as to the main points in their structure.

[2] The *Rachiopteris corrugata* of Williamson, "Organisation of Fossil Plants of Coal-measures," Part viii. *Phil. Trans. Roy. Soc.* vol. 167, 1876, p. 213, Figs. 1-24. The plant has proved to be quite distinct from *Tubicaulis*, with which I was once inclined to connect it.

on first leaving the stele, has a curved transverse section, concave outwards, as in *Tubicaulis*, and the H-like form is only very gradually assumed. The "Aphlebiae," which in this species are found chiefly in the petiole, have already been noticed (Fig. 117). The young leaves bear, in addition, a copious growth of ramenta.

The great peculiarity of *Z. corrugata*, as compared with the other three species in which the stem is known, consists in its mode of branching, which is not axillary, but rather of the nature of a dichotomy, the stem forking into two nearly equal branches without obvious relation to the leaf-insertion. This fact raises the question whether, as has been suggested, the apparent axillary branching of other species and of recent Hymenophyllaceae may not be a modified dichotomy, in which case the "undivided leaf-trace" would really be the stele of the smaller branch, and the "subtending" leaf would belong to this branch and not to the main axis. The data are insufficient to settle the question, and for the present it seems better to keep up the distinction between the two kinds of branching.

The adventitious roots of *Z. corrugata* are often well preserved; they are of relatively large size, usually with a diarch stele and a lacunar cortex.

The elements of the large-celled, peripheral wood in the stem of *Z. corrugata* occasionally show some tendency to a radial arrangement. In a fossil, provisionally placed in a new genus, *Botrychioxylon*, which in the structure of the internal xylem, the leaf-traces, and the mode of branching shows clear affinity with a *Zygopteris* of the *corrugata* type, the peripheral wood

is ranged in regular radiating series, and has all the appearance of a secondary tissue, precisely as in a recent *Botrychium*. The stele, in fact, is related to that of a *Zygopteris*, as the stele of *Botrychium* is related to that of *Ophioglossum*. *Botrychioxylon*, which may eventually have to be included under *Zygopteris*, at present affords the only instance of secondary growth of the wood among the Botryopterideae.

We now come to the interesting subject of the *fructification* of *Zygopteris*, our knowledge of which is almost entirely due to the researches of M. Renault.

The evidence of identification, if not absolutely conclusive, is at least sufficient to leave no reasonable doubt. The sporangia (see Fig. 119) occur in groups, often of considerable extent. They are elongated, slightly curved sacs, thickest towards the distal end, and of relatively large size, reaching a length of 2.5 mm. and a diameter of 1.3 mm. Each sporangium is attached by its thin end to a short pedicel; the pedicels are united in little tufts, three to eight in each tuft, on a common peduncle (Fig. 119, 1 and 2). The whole mass is traversed by fragments of a branched rachis, on which the peduncles were no doubt borne. In some sections of the rachis the characteristic H-like form of the *Zygopteris* bundle is clearly shown: "it is, then," to quote the words of M. Renault, "very probable, if not certain, that these masses of sporangia constitute the fructifications" of *Zygopteris*.[1]

The wall of the ripe sporangium consisted of at

[1] *Flore fossile d'Autun et d'Epinac*, Part ii. p. 43. The original discovery was made by M. Renault as early as 1876. "Veg. silicifiés d'Autun," *Ann. des sci. nat.* (*Bot.*), ser. vi. vol. iii.

least two layers of cells, of which the inner, more delicate layer has usually perished. The outer wall

FIG. 119.—*Zygopteris*, sp. 1. Group of four sporangia, on a common pedicel (*a*) × 10. 2. Two sporangia on pedicel. The upper shows the annulus (*c*) in surface-view, with spores exposed at *f*; the lower is in section. × 20. 2 *bis*. Sporangium, cut in plane passing through annulus. 3. Group of sporangia in transverse section. × 20. Lettering common to the figures: *a*, common peduncle; *b*, sporangial wall; *c*, annulus; *e*, tapetum (?); *f*, spores; *m*, pedicel of individual sporangium; *n*, probable place of dehiscence. All after Renault.

shows a marked differentiation; on two opposite sides it consists of small elongated cells, becoming fibrous

towards the base of the sporangium. But on the other two sides (alternating with the former) the cells are larger, with thicker walls, and with their maximum dimension vertical to the surface of the capsule (see Fig. 119). These larger cells thus form a vertical *annulus*, but one of a very peculiar kind, for it consists not of a single row of cells, but of a broad band, many cells in width (see Fig. 119, 2 and 3). At the summit of the sporangium the cells of the annulus thin out somewhat, so that we may regard it, if we like, as double, consisting of two distinct bands, one on each side. The pedicel is traversed, up to the base of the capsule, by a concentric vascular bundle, a condition very rare among recent Ferns, though approached in *Helminthostachys* and *Botrychium*. The pedicel, however, is best regarded as a branch of the rachis rather than as a sporangium-stalk.

Numerous spores are contained in the sporangia; they measure .08 mm. in diameter, which would be an ordinary size for the spores of recent Ferns. They are of the tetrahedral type, as is shown by the presence of the three radiating ridges, which are often visible on the exospore. M. Renault found other spores, of similar dimensions, in the same sporangia, which do not show the triradiate marking, but present a reticulate appearance, suggesting the presence of a group of polygonal cells within their cavity. This appearance has proved to be illusory, and the difference in the spores no doubt depends simply on their condition at the time of preservation, and is no indication of heterospory. The type of fructification is rather that of a homosporous member of the Filicineae. The leaves, or divisions of the

leaf, must have been dimorphic, for the branched rachis associated with the sporangia shows no signs of a lamina. We know, from numerous specimens preserved as impressions, that dimorphism was an exceedingly common phenomenon among the Ferns and Fern-like plants of the Carboniferous period. As to the form of the leaf, either sterile or fertile, beyond the fact that it was a compound one, we have no direct evidence from the silicified specimens.

Pear-shaped sporangia, with a very broad and extensive annulus, are commonly found associated with *Z. bibractensis* and *Z. corrugata* in the petrifactions of the English Lower Coal-measures, and in all probability represent the fructifications of those species.

M. Grand'Eury described, under the name of *Schizopteris*, specimens from the Coal-measures of the Loire, which are related to the structural specimens we have been considering. One of the forms described by Grand'Eury, *Schizopteris pinnata*, is a large bipinnate frond, with an apparently fleshy rachis, bearing small flabelliform and laciniate leaflets on its ultimate subdivisions. The author also described a *fertile* frond (*Schizostachys frondosus*) very similar to the former, but bearing tufts of elongated sporangia in the place of the laciniate leaflets of the sterile *Schizopteris*.[1] The arrangement, form, and size of these sporangia agree very closely with the characters of those described by Renault in his *Zygopteris*. The structure of the *Schizostachys* sporangia is to some extent preserved, and the spores are visible in their cavities. The agreement

[1] Grand'Eury, *Flore carbonifère du Département de la Loire*, 1877, pp. 198-203, Plate xvii.

in all points with the petrified specimens of *Zygopteris* is so exact as to make it certain that, as M. Renault first suggested, they belonged to some allied species of that genus. As it is also beyond doubt that *Schizopteris* and *Schizostachys* belonged together, we are enabled to form a fair idea of the external form of both the sterile and fertile leaves of *Zygopteris*. These fronds are included by Zeiller[1] in the latter genus, under the name of *Zygopteris pinnata*. Having inspected the fine specimens from Commentry in the collection of the École des Mines, I have no doubt that the attribution to *Zygopteris* is correct.

2. *Other Genera.*—The genus *Corynepteris* of Baily appears, according to Zeiller's investigations, to have been closely allied to *Zygopteris*. Several species have been described, and in some the form of the frond is well known. In certain of the species it is of the *Sphenopteris* type, resembling the frond of *Zygopteris pinnata*, but Pecopteroid fronds have also been found with a similar fructification. The sori are borne on pinnules, either like those of the sterile frond or comparatively little modified. The sporangia, so far as the annulus is concerned, are much like those of *Zygopteris*, but in most cases they are grouped in a ring round a centre, so as to resemble the synangium of an *Asterotheca*. *Corynepteris* thus, to a certain extent, combines the characters of Marattiaceae with those of Botryopterideae.[2]

[1] Zeiller and Renault, *Flore fossile de Commentry*, p. 76, Plate xxxii. Figs. 5-7, St. Étienne, 1888.

[2] For an account of the genus *Corynepteris*, see W. H. Baily, *Journal Geol. Soc. Dublin*, vol. viii. 1860; Zeiller, *Flore fossile du Bassin houiller de Valenciennes*, 1888, pp. 41 and 117.

Corynepteris is at present only known from impressions; we may compare with it a genus, *Diplolabis*, Renault,[1] which has been studied entirely in petrified material. The stem is unknown, but the structure of the petiole indicates affinity with *Zygopteris*. In both the species described, *D. forensis*, from the Upper Coal-measures, and *D. esnostensis*, of Lower Carboniferous age, the fructifications are described as synangia, with

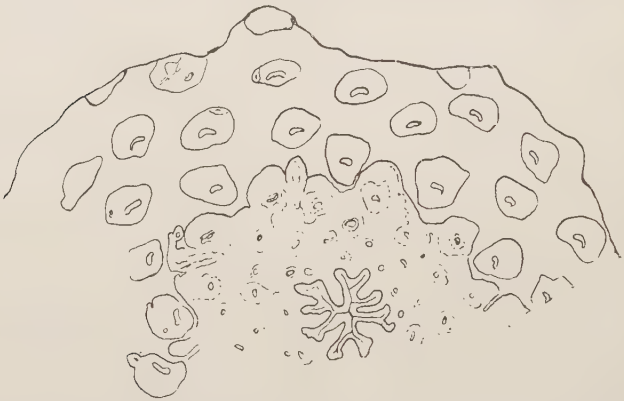

FIG. 120.—*Asterochlaena laxa.* Part of transverse section of stem with surrounding petioles. The deeply lobed stele is shown, also the leaf-traces and the curved bundles in the petioles. Nat. size. After Stenzel. From Tansley. *New Phytologist.*

from three to six sporangia attached to a common central receptacle. The sporangia differ from those of *Corynepteris* in having no differentiated annulus. It is also probable that the synangia were borne on a naked rachis, and not on an expanded lamina, as in the former genus.

Two genera, of which only the vegetative anatomy is known, may be shortly mentioned. *Anachoropteris*,

[1] *Flore fossile d'Autun et d'Epinac*, t. ii. p. 11.

from the Carboniferous and Permian, has a stem-structure (in *A. Decaisnei*, Ren.) almost identical with that of *Zygopteris Grayi*, but the petiolar bundle has quite a different shape, forming a strongly incurved arc, concave towards the parent stem. *Asterochlaena*, ranging from the Upper Devonian to the Permian, has a very deeply lobed stele, with the forked arms much more prominent than in *Zygopteris* (see Fig. 120). The protoxylem, in a section shown me by Mr. Kidston, appeared to be sunk below the projecting corners of the wood. The petiolar bundles are lunulate, with the concavity directed outwards or inwards, according to the species. Their relation to the stele has not yet been fully cleared up, and the interesting genus much needs reinvestigation.

B. Botryopteris Group

3. *Botryopteris.*—We will next consider *Botryopteris*, the type-genus of the family, and very distinct from the *Zygopteris* group. Our knowledge of this genus was, in the first instance, based on M. Renault's species, *B. forensis*, which that author described very thoroughly, though he had only a single specimen of the stem to work with.[1] Subsequently, however, it turned out that certain English Coal-measure fossils, which fortunately occur in considerable abundance, must be placed in the same genus. Hence we are able to supplement the descriptions of the original discoverer by observations on our own, specifically distinct, examples. Anatomically, *Botryopteris* shows a decidedly simpler structure

[1] *Cours de bot. foss.* vol. iii. chap. viii. ; *Ann. des sci. nat.* (*Bot.*), ser. vi. vol. i. 1875 ; *Flore fossile d'Autun et d'Epinac*, Part ii. p. 33.

than the former group. Here, as in the family generally, the stem is monostelic; the stele, however, is of a rather rudimentary type, consisting of a more or less cylindrical strand of solid wood, surrounded by phloëm, in which, in the English species (*B. ramosa* and *B. hirsuta*[1]), the large sieve-tubes are sometimes preserved. These two forms are very similar, and not always easy to distinguish, though it is possible that more than two species are concerned. *B. hirsuta* (Will.) had a small stem, about 2-3 mm. in diameter, and bore spirally arranged, somewhat crowded leaves, the petioles of which were at least equal to the stem in diameter. In *B. ramosa*, where the petioles, as a rule, are relatively smaller, the stem is usually larger than in *B. hirsuta*, sometimes reaching a diameter of 5-6 mm., while in the French species, *B. forensis*, it attains a diameter of 7.5 mm., in M. Renault's specimen. In all the species, the surface of the stem, and of the leaves also to some extent, was clothed by filamentous multicellular hairs, which, in the case of the French species, had a very peculiar structure, for each cell bore a ring of teeth at its distal end, giving the hair the appearance of a miniature *Equisetum*. This peculiarity proved of some importance in identifying the various organs of the plant.

The wood of the stem consists entirely of tracheides, mostly pitted, with a transition to scalariform structure, especially in the smaller elements. The proportion of the two kinds of tracheides is very variable in different specimens, and may prove to afford specific distinctions. The protoxylem is not always well

[1] *Rachiopteris ramosa* and *hirsuta* of Williamson.

marked; its position in the stem will be considered in connection with that in the petiole.

In the British species a $\frac{2}{5}$ phyllotaxis appears to have prevailed. The petiolar bundle is often actually larger than the stele of the stem, and contains larger

FIG. 121.—*Botryopteris hirsuta* (Will.). Transverse section of stem at its junction with the petiole; *x.s.*, xylem of stem; *x.p.*, xylem of petiole; r^1, r^2, diarch roots, springing from the stem; *h*, hairs. × about 15. (G. T. G.) S. Coll. 569.

tracheides (see Fig. 121). Its form, as seen in transverse section, is very characteristic. The elliptical band of xylem has three prominent points, all projecting on the same side, and directed towards the upper and inner face of the petiole. Hence the specific name *tridentata*, given to this petiole by Felix, before its

connection with *B. hirsuta* was known. The three prominent points (occasionally reduced to two) mark the position of the spiral protoxylem-elements. In some specimens the phloëm encircling the wood is exquisitely preserved.

Where the leaf-trace joins on to the vascular cylinder of the stem, its spiral tracheae are directed inwards. As, however, the bundle left the stele, it swung round, as it were (as often happens in recent Ferns also), taking up the position shown in Fig. 121. In M. Renault's type the form of the petiolar bundle is essentially the same as in the English species, but the structure is less simple and the three xylem-points are much longer, so that he compares the sectional form of the wood with that of the Greek omega (ω).

The structure of the cortex of the stem shows no striking differentation; in the petiole the outer cortical layers constitute a continuous sclerotic zone (Fig. 121).

The stem, in all the species, gave rise to very numerous diarch adventitious roots (Fig. 121, r^1, r^2), resembling those of many living Ferns.

In the petiolar bundle the position of the protoxylem is shown, not only by the presence of spiral tracheides at the prominent points, but also by direct developmental evidence, such as is rarely to be found in a fossil plant. In several cases a petiole or rachis has fortunately been preserved when still young, with its xylem only partially lignified, so that the small, thick-walled elements of the protoxylem, already differentiated, contrast sharply with the rest of the wood, in which the walls are still unthickened (see Fig. 122).

As the leaf-trace approached the stele its three

adaxial protoxylem-groups commonly united into one, and as fusion with the stele took place, this group necessarily took up an internal position in the stelar wood; every stage of the fusion is shown in serial sections of *B. hirsuta* or *ramosa*. Thus the xylem of the stele was endarch; spiral elements are not often to be found in the stem, which was a comparatively

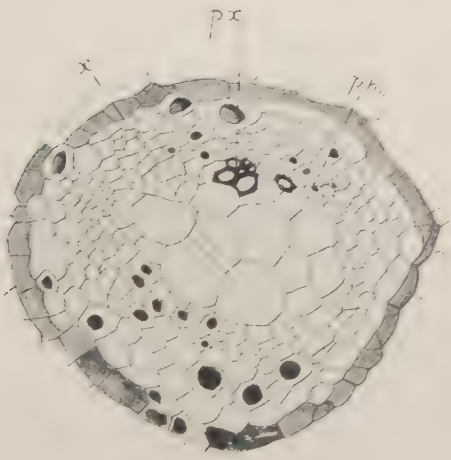

FIG. 122.—*Botryopteris hirsuta*. Transverse section of vascular bundle of young petiole, showing the xylem in course of differentiation. *px*, lignified protoxylem; *x*, thin-walled xylem not yet lignified; *ph*, phloëm-zone. The dark external layer may be the endodermis. × 150. S. Coll. 564. R. S.

short and presumably rather slow-growing rhizome. The small tracheides sometimes found at the periphery of the wood were probably in connection with the adventitious roots.

The rachis of the English species often shows branching, its branches being given off singly, and not in pairs as in *Zygopteris*, but such knowledge as we have of the form and structure of the lamina is entirely

derived from M. Renault's observations on the French specimens. The fine branches of the rachis had a simpler anatomical structure than the main petiole; they bore broad, lobed pinnules, with prominent veins, which branched repeatedly by dichotomy. The tissue of the lamina appears to have been fleshy; on the one

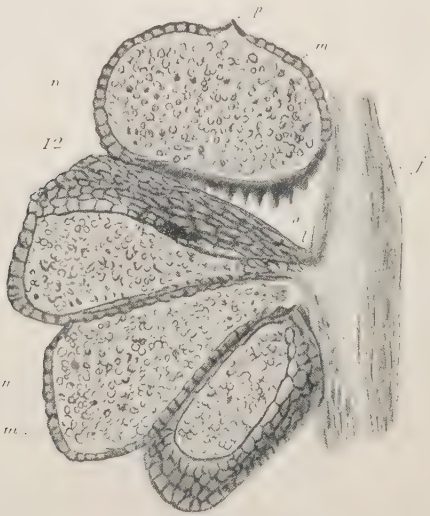

FIG. 123.—*Botryopteris forensis.* Group of sporangia, *m*, *m*, inserted on rachis, *j*; *l*, pedicel of sporangium; *n*, wall of sporangia; *o*, multiseriate annulus. The uppermost sporangium is in nearly transverse section; *p*, stomium, or place of dehiscence. × 35. From Renault.

surface numerous stomata were present, while the other bore the characteristic equisetiform hairs; it is on the latter feature that the identification of the leaf is based. M. Renault regards the stomatiferous surface of the leaf as the upper one, and supposes that the leaves of *Botryopteris* floated on the surface of the water, while other aërial leaves were borne by the same plant. These conclusions must be considered as highly hypothetical.

In one case M. Renault described a young frond in beautiful preservation, which was still circinately coiled, and bore numerous equisetiform hairs on its outer surface.

The *fructifications* of *Botryopteris forensis* bear a general resemblance to those of *Zygopteris*, but differ

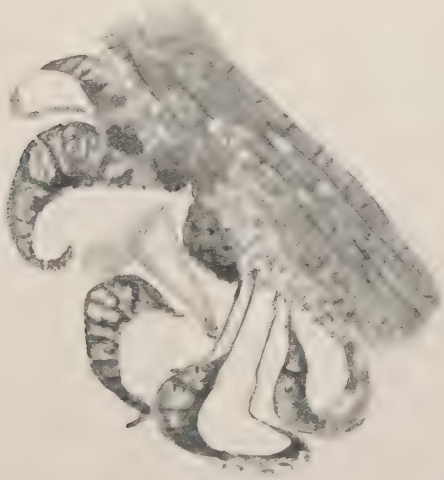

Fig. 124.—*Botryopteris.* Group of sporangia attached laterally to an axis, probably part of rachis. The sporangia show the multiseriate annulus; they have already dehisced. Associated with *B. ramosa.* Cf. Fig. 123. × 66. S. Coll. 776. R. S.

in detail. The sporangia occur associated in large masses, and crowded together, representing, no doubt, the collective output of a compound fertile frond. The pyriform sporangia are shortly stalked and grouped in tufts, on the branches of the fertile rachis (see Fig. 123). The latter shows in section the characteristic ω-shaped vascular bundle of the species, thus placing the identification beyond doubt.

The size of the individual sporangia is somewhat smaller than in Renault's *Zygopteris*, their length ranging from 1.5 to 2 mm., and their maximum diameter from .7 to 1 mm. The essential difference, however, from the sporangia of *Zygopteris* is in the annulus, which in *Botryopteris* was limited to one side of the capsule, where it formed a broad, oblique band of thick-walled cells (Fig. 123). The spores, except for their somewhat smaller size, agree exactly with those of *Zygopteris*, and, curiously enough, the same two states of the spore, already discussed in the case of that genus, recur here.

In one case a group of sporangia was found to be associated with a very curious envelope or indusium, of complicated structure, which M. Renault regarded as derived from a zone of sterile and highly modified sporangia.

It may be mentioned that the English specimens of *B. hirsuta* and *ramosa* are found associated with numerous sporangia, which appear to have essentially the same structure as those of the French species, but are of much smaller size. It is extremely probable that they represent the fructification of the English representatives of the genus. The association is close and practically constant, and as these species are among the commoner coal-ball fossils, this fact is of great weight. In one case the sporangia, which appear to have already dehisced, are found grouped on a rachis, as in Renault's specimens (see Fig. 124). They are, in the common form, of roundish shape, 350-400 μ in diameter, with a broad band of enlarged cells on one side, comparable to the false annulus of Osmundaceae (see Fig. 125). The somewhat triangular spores are characteristic.

4. *Other Genera.*—With *Botryopteris* we may compare another plant often found in the petrifactions of the English Lower Coal-measures, the *Rachiopteris cylindrica* of Williamson.[1] This has a slender stem, frequently branching by dichotomy, and occasionally bearing the bases of leaves. The preservation is often perfect; the stele resembles that of a small *Botryopteris*, but has a very well-marked central protoxylem-group. The leaf-trace bundles also bear some resemblance to those of *Botryopteris*, and the associated petioles are of a very similar type, *i.e.* the nearly straight bundle has the protoxylem-points all on the same side. The habit of the plant, with its long slender stem and, as it appears, very scattered leaves, must have been widely different from that of other Botryopterideae, and, though it has been proposed to include the species under *Botryopteris*, it may be preferable to found a new genus for it.

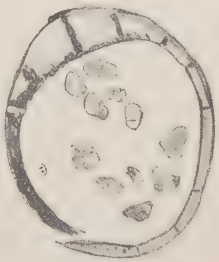

FIG. 125.—*Botryopteris.* Sporangium in transverse section, showing the multiseriate annulus, and containing some spores. Associated with *B. ramosa*. × about 100. S. Coll. 933. R. S.

Another genus closely allied to *Botryopteris*, and perhaps forming the simplest type of the family, is Renault's *Grammatopteris*, founded on a species, *G. Rigolloti*,[2] from the Permo-Carboniferous of Autun. The habit represents the opposite extreme to that of

[1] "Organisation of Fossil Plants of Coal-measures," Part ix. *Phil. Trans. Roy. Soc.* Part ii. 1878, p. 350, Figs. 80-87. Figs. 80, 86, and 87 are of the stem; the smaller sections appear to be of roots. For a more modern account see T. Hick, "On *Rachiopteris cylindrica*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. xli. 1896.

[2] *Flore fossile d'Autun et d'Epinac*, p. 45, Plate xxx. Figs. 9-11, Plate xxxi. Fig. 1.

the plant last described, for the crowded petioles here form a dense envelope round the stem. The stele has a solid cylinder of xylem, as in *Botryopteris*; the spiral elements are stated to be at the periphery, but this requires further investigation. The leaf-traces and petiolar bundles have the form of a straight tangential band, described as having the spiral elements at the two ends. The genus is imperfectly known. Small sporangia of the *Zygopteris* type were found by Renault in association with the plant, but there is no proof of connection.

The genus *Tubicaulis*, as now limited, has a remarkable history. Only two specimens referable to it have ever been discovered; one was found in the Permian of Saxony in 1815, and described by Cotta in 1832;[1] the other was found by Mr. Lomax a couple of years ago in a roof-nodule in the Lower Coal-measures of Shore, Lancashire, and described by Miss Stopes in 1906.[2] The two specimens are, of course, specifically distinct. The Permian species is *T. Solenites*, Cotta; that from the Coal-measures is named *T. Sutcliffii*, Stopes. Both were large plants; the specimen of *T. Solenites* was, when found, a yard long, and from 5 to 8 inches in diameter, most of this thickness being made up of the crowded leaf-bases and petioles, while the fragment representing *T. Sutcliffii* had a diameter of $2 \times 4\frac{1}{2}$ inches. The structure of the stem is excessively simple, the stele having a solid cylindrical strand of xylem, which Miss Stopes believes

[1] *Die Dendrolithen in Beziehung auf ihren inneren Bau*, p. 21, Taf. ii.

[2] "A New Fern from the Coal-measures: *Tubicaulis Sutcliffii*, spec. nov.," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. l.

to have been wholly or chiefly centripetal in development. The petioles, which increased rapidly in diameter after leaving the stem, contain a horse-shoe bundle, with the concavity outwards; the protoxylem groups clearly lie on the convex, adaxial side. The numerous adventitious roots are diarch. Small sporangia, much like those attributed to the British species of *Botryopteris* (Fig. 125) are associated with the specimen, and as no other plant is present in the nodule, this association has some significance.

The three forms last described, *Rachiopteris cylindrica*, *Grammatopteris*, and *Tubicaulis*, are evidently closely allied to *Botryopteris*, and, together with that genus, constitute a sub-family, with which the *Zygopteris* group, including *Anachoropteris* and *Asterochlaena*, may be contrasted. The great distinction lies in the stele, a simple cylindrical column with solid xylem in the Botryoptereae, while in the Zygoptereae it has usually a more complex form, and appears always to have a double xylem, with the small internal tracheae accompanied by parenchyma. There is no constant distinction in the petiolar bundle, though here also the Zygoptereae tend to complexity, but the double series of rachis-branches appear to be characteristic of the *Zygopteris* group. There can be no doubt that the latter are the more highly organised, and the Botryoptereae presumably, although not certainly, the more primitive. It must be remembered that *Asterochlaena*, which clearly falls into the *Zygopteris* division, is, on present evidence, the most ancient of the whole family. The two groups have so much in common (especially in the

fructification, where known) that their association in a single family is fully justified.

We have still to consider a genus which at present stands a little apart from the rest of the family.

5. *Stauropteris.* — The best-known species, *S. oldhamia*, Binney, is one of the commonest fossils of the Coal-measure nodules; a very similar species, of Lower Carboniferous age, has recently been named *S. burntislandica* by M. Paul Bertrand. We will confine our attention to the former.

The stem is unknown; the specimens consist of fragments of the petiole and rachis of a highly compound frond, without any recognisable lamina, but bearing sporangia on its ultimate branches. In the large petioles the xylem has a characteristic cruciform section, while the whole stele is approximately square, the phloëm filling up the bays between the xylem-arms, and sometimes extending to the centre, so as to interrupt the continuity of the wood (Fig. 126). The example figured is tetrarch; often, however, there is more than one protoxylem-group at each angle, though this condition may be correlated with the branching. As M. P. Bertrand has observed, the protoxylem is sunk a little below the surface of the wood, which is therefore not strictly exarch. The phloëm contains large sieve-tubes, and the sieve-plates on their lateral walls are sometimes clearly shown. A lax, palisade-like tissue occurs below the epidermis, and probably had the function of assimilation. The branches were given off in pairs, successive pairs springing from opposite sides of the rachis, a mode of branching

recalling that of the *Zygopteris* petioles. The branches are of many orders; those of intermediate dimensions have a three-armed xylem, while the excessively fine terminal ramifications are traversed by a bundle of correspondingly simple structure. Certain slender strands which are given off concurrently with the

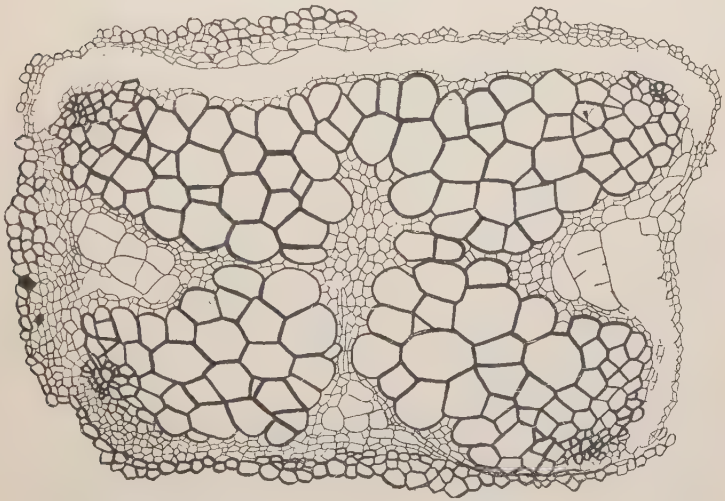

FIG. 126.—*Stauropteris oldhamia.* Transverse section of vascular bundle of main rachis, showing the cruciform xylem with protoxylem near the four angles. Groups of large sieve-tubes are seen in the bays of the wood, and small-celled phloëm between wood and cortex. × 60. S. Coll. 2202. From Tansley, *New Phytologist.*

main branches are described by M. P. Bertrand as supplying aphlebiae—another point of analogy with *Zygopteris.*

It was on the delicate ultimate branches of the rachis that the terminal sporangia were borne (Fig. 127). The fronds at present known appear to be all fertile; whether other vegetative leaves also occurred, or the foliage was of an extreme xerophytic type, with the

laminae wholly suppressed, cannot yet be determined. The analogy of *Zygopteris* and *Botryopteris*, however, speaks strongly for the former hypothesis.

The sporangia are nearly spherical sacs, about .7 mm. in diameter, with a wall several cells thick and the outermost layer strongly differentiated. There is no annulus, but a well-marked stomium at the end

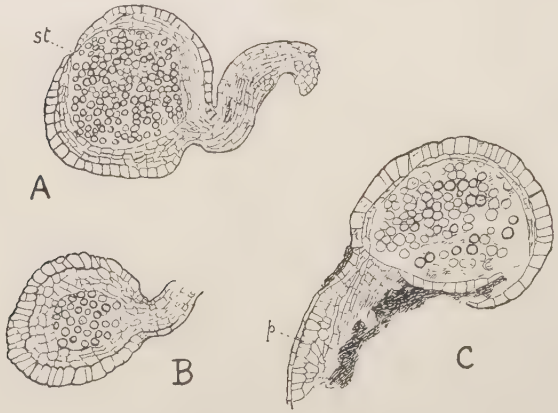

FIG. 127.—*Stauropteris oldhamia*. Three sporangia inserted terminally on ultimate branches of the rachis. In A the stomium, *st*, is shown. B is cut tangentially. In C, *p* is the palisade-tissue of the rachi. The relatively large spores in C are probably beginning to germinate. Cf. Fig. 128. × about 35. S. Coll.; A, 2213; B, 2207; C, 2219. R. S.

opposite the stalk (Fig. 127, A) served for dehiscence. Numerous spores of the tetrahedral type fill the cavity.

At the time when these sporangia were first discovered,[1] the question was left open whether the plant was a Fern or a Pteridosperm, for there was nothing to show for certain whether the fructification represented

[1] Scott, "The Sporangia of *Stauropteris oldhamia*," *New Phytologist*, vol. iv. 1905.

homosporous sporangia or microsporangia. A year previously a case had been observed in which spores were found germinating inside an isolated sporangium, the stages agreeing with those found in recent Ferns.[1] Subsequently, similar stages of germination were detected in typical sporangia of *Stauropteris oldhamia*, establishing a strong presumption that this plant also was a true homosporous Fern.[2] Some of the germinat-

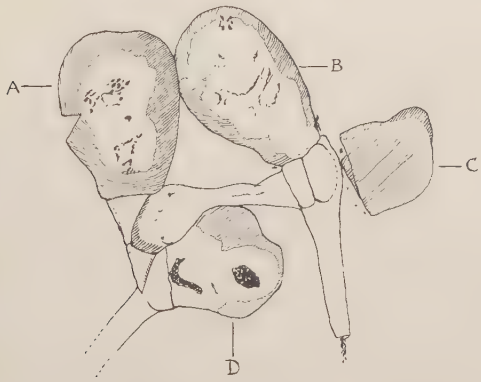

FIG. 128.—*Stauropteris oldhamia*. Four germinating spores from the interior of a sporangium. All four are putting out rhizoids. In C (lying horizontally) an additional cell has been cut off between rhizoid and spore. × 335. S. Coll. 2215. Drawn by Mr. L. A. Boodle.

ing spores are shown in Fig. 128. All four have sent out rhizoids, cut off by a wall from the body of the spore, and in C another cell has been cut off above the rhizoid. In the light of these observations there is no longer any reason to doubt that *Stauropteris* was

[1] Scott, "Germinating Spores in a Fossil Fern-Sporangium," *New Phytologist*, vol. iii. 1904.

[2] Scott, "The Occurrence of Germinating Spores in *Stauropteris oldhamia*," *New Phytologist*, vol. v. 1906. I am indebted to my wife, Mrs. D. H. Scott, F.L.S., for much help in these observations.

really a Fern, while the analogies with *Zygopteris* and other Botryopteridcae are sufficiently close to justify us in classing the whole family with the Ferns. I am inclined to agree with the Messieurs Bertrand that the affinity between *Stauropteris* and *Zygopteris* is a fairly near one. At the same time, the absence of an annulus from the sporangia of the former marks a real distinction, though it will be remembered that *Diplolabis*, a genus also betraying some affinity with *Zygopteris*, has the same peculiarity.

6. *Affinities of the Family.*—The habit, anatomy, and sporangial characters all point to the Botryopteridcae having been true Ferns. The germinating spores of *Stauropteris*, agreeing so closely with the corresponding stages in recent homosporous Ferns, raise this presumption almost to a certainty, and there is at present no countervailing evidence to be weighed.

We have now to consider, very briefly, the question of the probable affinities of the group with other Filicales.

The fructification, on which one would naturally lay the chief stress, appears to remove the family from any of the more typical groups of Leptosporangiate Ferns. The size and form of the sporangia are too variable to be characters of any importance, but the annulus, when present, has definite peculiarities. In the genera *Zygopteris* and *Botryopteris* it forms a well-defined longitudinal or oblique *multiseriate* band of cells, occurring on both sides of the sporangium in *Zygopteris*, on one side only in *Botryopteris*. The nearest analogy among recent Ferns is perhaps to be

found in Osmundaceae, where the annulus is represented by a unilateral group of thickened cells, the areola, resembling the *Botryopteris* arrangement in a reduced form.

On the other hand no annulus is differentiated in *Diplolabis* or *Stauropteris*, genera which were certainly allied to the Botryopterideae, though this character would exclude them from the family as defined by Renault.[1] The annulus evidently afforded less constant characters among Palæozoic Ferns than is now the case.

The position of the sporangia in *Zygopteris*, *Botryopteris*, and *Stauropteris*, where they are terminal on ultimate branches of the rachis, is not very closely paralleled among recent Ferns, but finds its nearest analogy in *Helminthostachys* and *Botrychium* among the Ophioglossaceae,[2] the comparison being closest with the case of *Botryopteris* (Fig. 123).

The dimorphism of the fronds, though so striking a character, is not of the first importance, for we know that it recurs in almost every group of living Ferns, and that within the same genus some species may be dimorphic, while in others there is no differentiation between the sporophylls and the ordinary foliage.[3]

At the same time the great modification of the fertile frond in *Zygopteris*, *Botryopteris*, *Stauropteris*,

[1] *Flore fossile d'Autun et d'Epinac*, t. ii. p. 33, 1896.

[2] See Bower, "Spore-producing Members. II. Ophioglossaceae," Plate v. Fig. 81.

[3] The word dimorphism is used to include both the differentiation of sterile and fertile leaves, and that of sterile and fertile parts of the same leaf. In the case of fossil Ferns it is usually impossible to say which was the case, and among recent Ferns the distinction is not always constant, even in the same species.

and probably *Diplolabis*, is of importance as evidence against any direct connection between these genera and the Ferns of later periods. Among the latter dimorphism has appeared in most of the families, but, except in the Ophioglossaceae, it is never a family character. There is a strong presumption that in Hymenophyllaceae, Schizaeaceae, Osmundaceae, Cyatheaceae, and Polypodiaceae uniformity of foliage is a more primitive condition than specialisation of sporophylls, and that each of these families, as well as the Gleicheniaceae and Marattiaceae, started with sporangia borne on the ordinary frond. If this be so, it implies that the typical Botryopterideae cannot have been on the direct line of descent of the Lepto-sporangiate Ferns.

Vegetative, and especially anatomical characters, must also carry considerable weight. The monostelic structure, and the single petiolar bundle, suggest a comparison with one of the four families, Osmundaceae, Schizaeaceae, Gleicheniaceae, and Hymenophyllaceae. The axillary shoots of *Zygopteris* indicate the last-named group as that with which the analogy is most evident, and other anatomical features confirm this indication. The resemblance between the anatomy of one of the larger species of *Trichomanes* and that of *Zygopteris* is in fact very striking.[1] The stele of *Trichomanes reniforme*, for example, has a simpler form than that of the main stem in *Z. Grayi*, but the arrangement of its elements is much like that in the fossil plant,

[1] See L. A. Boodle, "Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae, and Gleicheniaceae. I. Hymenophyllaceae," *Ann. of Bot.* vol. xiv. 1900.

and if we consider the axillary shoot of the latter, where the stele has a simple bilateral structure, the agreement is almost exact. The protoxylem of *T. reniforme* is placed internally, forming two groups, accompanied by parenchyma, while small elements also occur at the periphery of the wood, where they are connected with the insertion of adventitious roots. In other species, however, the protoxylem may be wholly peripheral (*e.g. T. scandens*) or scattered (*e.g. T. spicatum*). The leaf-trace gives off the stele of the axillary branch precisely in the same manner as in *Zygopteris*, the resemblance extending even to details. It would be rash to push the comparison too far, but, from an anatomical point of view, there is no doubt that the Hymenophyllaceae show the closest analogies with the genus *Zygopteris*, and especially with those species which have axillary branching. With *Botryopteris* there is also a general agreement, though a much less close one. As Mr. Boodle says (*loc. cit.* p. 489), "The solid stele of *Botryopteris*, as the wood consists of tracheides only, resembles the stele found in the lower part of the seedling-stem of *Trichomanes* rather than the solid stele of *T. spicatum*, etc." The general analogy between Botryopterideae and Hymenophyllaceae was early recognised by Renault. It is, however, improbable that anything more than a remote affinity is indicated by the analogies referred to.

As already pointed out, there is a fairly sharp distinction between the anatomy of the *Botryopteris* type and that represented by *Zygopteris*. The former, so far as the stem is concerned, is perhaps the simplest in any known vascular plant, though many

circumstances forbid us to assume that this simplicity is primitive. The *Zygopteris* type of stele is far more complex, and an interesting point is that its structure lent itself to secondary growth, so that in *Botrychioxylon* we find the primary wood replaced by secondary, just as is the case in *Botrychium* as compared with *Ophioglossum*. Of course nothing more than an analogy is suggested here, for the internal xylem of the *Zygopteris* group is unrepresented in the recent family. Still it is quite possible that some real affinity may exist.

The Botryopterideae may fairly be called a synthetic group, in so far as they show analogies with a number of families of later origin. Attention has already been called to points of resemblance between them and the Hymenophyllaceae, Osmundaceae, and Ophioglossaceae. They have also been compared with Schizaeaceae on account of the biseriate annulus sometimes observed in that family, though differing in position from that in our fossils; anatomically a basis of comparison may be found in the internal tracheides occurring in the stele of *Schizaea malaccana* and other species.[1] If *Corynepteris* is rightly associated with Botryopterideae, the synangia suggest a relation to Marattiaceae; the fructification of *Diplolabis* points in the same direction, and *Sturiella* (Fig. 109, D) may also be regarded as combining Marattiaceous with Botryopteridean characters.

In the first edition of this book I expressed the opinion that the Botryopterideae not improbably

[1] Tansley and Chick, "Structure of *Schizaea malaccana*," *Ann. of Bot.* vol. xvii. 1903; Boodle, "Comp. Anat. of Hymenophyllaceae, Schizaeaceae, and Gleicheniaceae. IV. Further Obs. on *Schizaea*," *ibid.*

represented the stock from which some at least of the existing families of Ferns were subsequently derived. Mr. Kidston has recently made a similar suggestion, regarding the descent of Leptosporangiate Ferns from the Botryopterideae as much more probable than from any other Palæozoic group so far as known to us at present.[1] Mr. Arber,[2] taking a somewhat broader view, derives the Leptosporangiatae from an ancient Palæozoic race, which he names the Primofilices, of which the Botryopterideae were but one important family. He further suggests (*loc. cit.* p. 227) that possibly the origin of the Eusporangiatae is also to be sought for in the group termed the Primofilices. I regard Mr. Arber's views as an advance on those previously held. The Botryopterideae, or at least their better-known members, appear too specialised to have themselves been the ancestors of the modern Ferns, but the analogies which they present with so many families of the latter indicate that they are probably an offshoot from the same main line of descent. Kidston and Gwynne-Vaughan, in discussing the comparative anatomy of Osmundaceae and Botryopterideae, state that they "regard the Osmundaceae as directly descended from an ancestral stock from which at least two other types of structure arose—that of *Botryopteris* and that of *Zygopteris*,"[3] a conclusion entirely in harmony with the general view indicated above.

[1] "On the Microsporangia of the Pteridospermeae," *Phil. Trans. Roy. Soc.* B, vol. cxcviii. 1906, p. 442.

[2] "On the Past History of the Ferns," *Ann. of Bot.* vol. xx. 1906, p. 221.

[3] R. Kidston and D. T. Gwynne-Vaughan, "On the Fossil Osmundaceae," Part i. *Trans. Roy. Soc. Edinburgh*, vol. xlv. Part iii. 1907.

The possible affinities of Botryopterideae in other directions than that of the Ferns will be considered later on.

II. Summary

The general conclusion to which we are led by a consideration of the evidence bearing on the existence of Ferns in the Palæozoic period is that this class was then fairly well represented, though by no means holding the dominant position formerly assigned to it. On the one hand we have, as a characteristic group, the remarkable family of the Botryopterideae, very different from any of the more modern families of Ferns, though presenting analogies with them in various directions. On the other hand, we have the Marattiaceous type, much more complex in anatomical structure, and with clear affinities to the recent Ferns of that group. The doubts that have lately been cast on the authenticity of Palæozoic Marattiaceae have been suggested by the similarity between supposed Marattiaceous fructifications and the pollen-bearing organs of certain Pteridosperms and Cycadophyta. In the absence of anatomical evidence we are doubtless often left in uncertainty whether a given fructification is to be referred to the one category or the other. The structure of the *Psaronius* stems, however, appears conclusive as to the existence of a considerable group of true Palæozoic Marattiaceae, to which, no doubt, many of the fronds bearing synangia belonged.

Mr. Arber's proposed group, the Primofilices, embracing all the more primitive Palæozoic Ferns, with the

Botryopterideae as at present the best-known family, has already been referred to, and the idea is likely to be a fertile one. We are not, as yet, in a position to fill in the features of this ancient race, for outside the Botryopterideae themselves, or their immediate allies, our knowledge of such Ferns is scanty. But, as Mr. Arber points out, many of the Fern sporangia of the petrifactions will doubtless find their place here, and so, perhaps, will some of the fructifications, such as *Oligocarpia* or *Senftenbergia*, which have been provisionally referred to definite recent families. *Pteridotheca Williamsonii* (Fig. 112, p. 293) is a good example of a Palæozoic Fern with annulate sporangia borne on leaflets of an ordinary vegetative type, and there are several similar cases. Various families of Ferns are known to have been well developed in the Mesozoic Period, and their ancestors must have been present in Palæozoic times. For reasons already given, I can no longer regard the Botryopterideae as lying on the direct line, but some of the forms of "Primofilices" with non-specialised sporophylls may well have been nearer the progenitors of Ferns as we know them.

The genus *Corynepteris* suggests a possible connection between the Primofilices and the Marattiaceae, an hypothesis which, indeed, is almost inevitable on general grounds. The Ferns grouped under Primofilices, as this name is intended to imply, are of great antiquity, occurring commonly in the Lower Carboniferous (various Botryopterideae) and extending back to the Devonian (*Asterochlaena*), while the Marattiaceae are not known to be older than the Upper Carboniferous (Lower Coal-measures).

It is doubtful if the distinction between Eusporangiate and Leptosporangiate Ferns existed in Palæozoic times—in other words, whether the development of the sporangium from a single cell had yet been arrived at. In the Botryopterideae, at any rate, it is improbable that this was the case, the mode of insertion of the sporangia, and their large size in many cases, pointing to a multicellular origin.

The conclusions of Professors Campbell and Bower, as to the relative antiquity of the Eusporangiate type, are thus amply justified by palæontological evidence. On the other hand, it may be doubted whether this evidence justifies the view that the confluent synangium was a primitive form of Fern-fructification. Many Palæozoic Marattiaceae, it is true, possessed synangia, but, on the whole, the sporangia of which they were composed were less completely united than in most of the recent members of the family. While in *Ptychocarpus* the cohesion was complete, in *Scolecopteris*, *Asterotheca*, *Sturiella*, and the *Grand'Eurya* of Stur the individual sporangia enjoyed a considerable measure of independence. Neither were the Marattiaceae by any means the most ancient Ferns. The Botryopterideae were older, and had, in most cases, free sporangia. Among the fairly numerous Fern-sporangia preserved in the petrified material of the British Lower Coal-measures and Lower Carboniferous rocks, it is rare to find any signs of cohesion. The fossil evidence, on the whole, supports the view that free sporangia represent the original form of Filicinean fructification, and that their cohesion to form synangia was

a secondary modification, though one which, in certain groups, took place at a very early period.[1]

From an anatomical point of view, two main types of stem are sharply distinguished among the Palæozoic Ferns. On the one hand, we have the large, highly complex, polystelic stems represented by *Psaronius*, and belonging, no doubt, to the Marattiaceous Tree-ferns. On the other, we have the herbaceous monostelic forms, such as the Botryopterideae.

The monostelic group is generally further characterised by having only a single vascular bundle in the petiole, and it is remarkable that this peculiarity also extended to many of the polystelic forms (species of *Psaronius*), which, in the simplicity of their petiolar structure, differed widely from Marattiaceae, while agreeing with them in the anatomy of the stem. On the evidence now available, it appears that monostelic structure of the stem was more common among Palæozoic than among recent Ferns, while monodesmic structure of the petiole was the rule,[2] though not, of course, without exceptions. Summing up the results, we may say that the Palæozoic, or at least the Carboniferous Ferns, group themselves anatomically into two main cycles—the Palæo-Marattiaceae on the one hand, and on the other that great synthetic group of Ferns (Primofilices) with a simple anatomical

[1] Stur came to a similar conclusion, "Culm- und Carbonfarne," p. 161. See, however, F. O. Bower, "Studies in the Morphology of Spore-producing Members," iii. Marattiaceae, *Phil. Trans. Roy. Soc.* 1897, B, p. 35, for an able statement of the opposite view; also his *Origin of a Land-Flora*, p. 523, 1908.

[2] See L. A. Boodle, "On the Comp. Anatomy of Hymenophyllaceae, Schizaeaceae, and Gleicheniaceae," *Ann. of Bot.* vol. xiv. 1900, vol. xv. 1901, vol. xvii. 1903.

structure, of which we may take the Botryopterideae as the best-known examples.

Space forbids us to extend our studies to the Ferns of later epochs. It may be interesting, however, to point out that during the Mesozoic period nearly all the different groups of recent Ferns made their appearance.

Among the Marattiaceae, the Palæozoic genus *Asterotheca* has been found to persist in the Triassic and even Rhaetic beds. On the other hand, specimens from the Rhaetic and the Lias have been referred to the recent genera *Marattia* and *Danaea*.

Gleicheniaceae have been identified as far back as the Lias, and perhaps the Trias.

One of the most curious features of the Fern-vegetation throughout the Secondary period is the prominence of the family Matonineae, now represented by a single genus, with two species, *Matonia pectinata* and *M. sarmentosa*, plants of limited distribution in the Malayan region. This group, which combines the characters of Cyatheaceae and Gleicheniaceae, can be traced back, on evidence derived from the fructifications as well as from foliar characters, at least as far as the Rhaetic beds.[1]

Cyatheaceae can be identified as far back as the Lias, and Schizaeaceae are found in the Jurassic.

Osmundaceae have been recognised by their fructifications in the Rhaetic and Trias, and fossils from these rocks have even been referred to the recent genera *Osmunda* and *Todea*.

[1] See Seward, "On the Structure and Affinities of *Matonia pectinata*, with Notes on the Geological History of the Matonineae," *Phil. Trans. Roy. Soc.* vol. 191, B, 1899.

The fossil history of the Osmundaceae from an anatomical point of view is now being investigated by Kidston and Gwynne-Vaughan. Among the forms already dealt with, the *Osmundites skidegatensis* of Penhallow, from the Lower Cretaceous of Queen Charlotte Islands, British Columbia, may be mentioned. The preservation is astonishingly perfect and the stem is remarkable for possessing a well-developed internal phloëm. This feature, however, was found to be absent from the still older members of this family.

There appears to be little satisfactory evidence as yet as to Mesozoic Hymenophyllaceae.

The family Dipteridineae, formerly included under Polypodiaceae, appear to have a long geological record, Ferns referred to this group having been found in the Lias, Rhaetic, and Trias.[1]

True Polypodiaceae have not been traced further back at present than to Jurassic rocks.[2]

The palæontological data just cited may be compared with the arrangement of the families of Ferns, proposed by Professor F. O. Bower,[3] on the basis of an exhaustive investigation of the development of the sorus, and the output of spores. The main lines of his classification are exhibited in the following table :—

[1] Seward and Dale, "On the Structure and Affinities of *Dipteris*, with Remarks on the Geological History of the Dipteridineae," *Phil. Trans. Royal Soc.* B, vol. 194, 1901.

[2] For a fuller summary see Zeiller, "Les Progrès de la Paléobotanique de l'Ere des Gymnospermes," *Progressus Rei Botanicae*, vol. ii. 1907.

[3] "Studies in the Morphology of Spore-producing Members," iv. The Leptosporangiate Ferns, *Phil. Trans.* vol. 192, B, 1899. For a more recent statement, see his *Origin of a Land-Flora*, 1908, especially the scheme on p. 653.

FILICES—Isosporeae

Simplices	Marattiaceae.	*Eusporangiate.*
	Osmundaceae.	
	Schizaeaceae.	
	Gleicheniaceae.	
	Matonineae.	
Gradatae	Loxsomaceae.	*Leptosporangiate.*
	Hymenophyllaceae.	
	Cyatheaceae.	
	Dicksonieae (with some exceptions).	
	Dennstaedtiinae.	
Mixtae	Davallieae (with some exceptions).	
	Lindsayeae.	
	Pterideae and other Polypodiaceae.	

The Simplices are those Ferns in which all the sporangia of a sorus are produced simultaneously, the Gradatae those in which there is a definite succession in time and space, the Mixtae those in which there is a succession in time, but no regular succession in space.

Other characters of importance coincide more or less with the above; for example, the sporangia tend to become smaller, with fewer spores in each, as we advance from the Simplices to the Mixtae.

It will be seen that the geological evidence, so far as it goes, harmonises well, on the whole, with the main divisions in Professor Bower's system. The old distinction between Eusporangiatae and Lepto-

sporangiatae takes a secondary place, and to this the palæobotanist can make no objection, for on existing evidence it is doubtful whether the distinction existed among Palæozoic Ferns.

A remarkable lacuna in our knowledge of the older fossil Filicales is the entire absence, so far as is yet ascertained, of any satisfactory evidence for the existence of heterosporous forms. Fossil Rhizocarps have often been described, but, so far as the earlier strata are concerned, on the most questionable evidence.

There are strong reasons for supposing that heterospory must have appeared among Ferns in Palæozoic times, but this question will be considered in the last chapter of the book.

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